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PHYTOPHTHORA TRUNK CANKER OR COLLAR ROT OF APPLE TREES[1]

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INTRODUCTION

Trunk cankers have long been known to cause severe losses of trees in Indiana apple orchards. In some cases the damage has resulted from winter injury, or has been caused by fire blight (*Erwinia amylovora* (Burr.) Comm. S. A. B.). However, the cause of a particular type of destructive canker on the trunks of apple (*Malus sylvestris* Mill.) near the soil line, which occurs primarily on the Grimes Golden variety in Indiana, has not been definitely known. Following a serious epidemic of this type of collar rot in 1933, investigations of the nature of the disease and its control were undertaken. *Phytophthora cactorum* (L. and C.) Shroet. was found to be the causal agent. This paper presents the results of studies of the pathogenicity and physiologic specialization of the causal fungus, resistance and susceptibility of the host, and means of control of the disease.

THE DISEASE

HISTORY

Cankers caused by *Phytophthora cactorum* on the trunks of Grimes Golden trees, described by the writer (*3*, *5*),[3] are similar in many respects to collar rot cankers of undetermined or doubtful origin reported by several investigators. As early as 1858 the dying of apple trees as a result of an injury to the bark on the trunk and collar received considerable attention from fruit growers. According to Bradford and Cardinell (*7*), T. T. Lyon in addressing a meeting of horticulturists at Kalamazoo, Mich. in 1858, advocated the double-working of trees as a means of avoiding winter injury of the tender varieties. They mention that Baldwin, Tompkins King, Roxbury Russet, Rhode Island Greening, Esopus Spitzenburg, Hubbardston, and particularly Grimes Golden have long been listed as susceptible to collar injury. Stewart, Rolfs, and Hall (*43*), in 1900, described a collar rot of several varieties of apple trees in New York. They mentioned that the Tompkins King variety was so susceptible to attack that the disease was generally known as the king disease. Grossenbacher (*17*, *18*), in 1909 and 1912, reported investigations on the nature of collar rot on apple trees in New York, and presented a review of the literature on this subject. He did not agree with Headden (*19*, *20*) that arsenical poi-

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[3] Italic numbers in parentheses refer to Literature Cited, p. 182.

soning was the cause of collar rot, but was of the opinion that much of the injury was induced by low winter temperatures. In 1926 Thomas (*44*) concluded that low winter temperatures caused a root and crown injury on apple trees in New York.

Collar rot of doubtful or unknown origin has been reported frequently. Selby (*37*), in 1900, in general attributed collar rot of apple trees in Ohio to winter injury. He mentioned that Grimes Golden, Tompkins King, and some other varieties, even in ordinary winters, seem to die on one side of the trunk just above the surface of the ground. Since the injury was not always confined to the south or southwest side of the trees, he expressed some doubt that it resulted entirely from the effects of winter temperatures. In an earlier bulletin (*36*) he reported that two orchards of 8- to 10-year-old Baldwin trees were ruined by winter freezing in 1881, while Grimes Golden trees under the same circumstances escaped. In 1913 Selby (*38*) stated that the very serious collar rot of Grimes Golden trees can be largely overcome by using top-grafted rather than root-grafted trees. Later, in 1921, Selby [4] and in 1922 Thomas,[5] reported a collar rot of undetermined origin on Grimes Golden and certain other varieties in Ohio. In reply to a question on collar rot, during a meeting in 1900 of the Indiana Horticultural Society, Burton (*8, p. 66*) stated:

> It is quite likely that Mr. Tilson is troubled with what I term Grimes' bark disease. It is very much subject to bark disease, which affects it at the ground or a little above it. I don't know of any other tree so affected * * *.

In 1921 Gardner (*15*) reported one orchard in southern Indiana in which approximately 25 percent of the Grimes Golden trees were affected with a collar rot, the cause of which was unknown. The disease appeared to be particularly serious on trees between 20 and 25 years of age. Anderson (*1*), in 1917, attributed a collar rot of Grimes Golden in Illinois to winter injury. However, the symptoms which he described are similar to those caused by *Phytophthora cactorum*. In 1918 Anderson (*2*) stated that collar rot, or Grimes Golden disease, appeared in orchards after the trees were about 10 years old, and frequently developed so rapidly that by the twentieth year, two-thirds of the Grimes trees were dead or in a dying condition. He suggested that double working or high grafting might offer a solution of the trouble. In 1919 collar rot of Grimes Golden trees in Illinois was adjudged to be a physiological condition, since attempts to isolate a causal organism failed (*23*). Anderson [6] reported that in 1920 collar rot caused a crop loss of 1 percent in Illinois. Grimes Golden was the principal variety attacked. Anderson stated that the exact cause was unknown, but was probably winter injury.

Hotson (*22*), in 1920, concluded that most of the collar-rot cankers in the Yakima Valley, Wash., were due to fire blight, though the evidence that he presented was largely circumstantial. He listed a number of causes of collar rot, and stated that in the Yakima Valley comparatively few of the cankers can be traced to winter injury. As in many of the other publications reviewed, no mention was made of varieties affected. Magness (*26*), in 1929, concluded that low winter temperatures were the main cause of injuries occurring on the base of the trunks and roots of apple trees in Washington. He did not be-

[4] ANDERSON, H. W. DISEASES OF FRUIT CROPS IN THE UNITED STATES IN 1920. U. S. Bur. Plant Indus., Plant Disease Bull. Sup. 14:1–114. 1921. [Mimeographed.]

[5] HASKELL, R. J., and WOOD, JESSIE I. DISEASES OF FRUIT AND NUT CROPS IN THE UNITED STATES IN 1921. U. S. Bur. Plant Indus., Plant Disease Bull. Sup. 20:1–138. 1922. [Mimeographed.]

[6] See footnote 4.

lieve that fire blight, as reported by Hotson (*22*), was an important contributing factor. A collar rot occurring on 15 varieties of apple trees in Pennsylvania was described by Orton and Adams (*29*) in 1915. They isolated the fire-blight organism from many of the cankers, and reported that typical cases of collar blight resulted from artificial inoculations into the collar and roots of young apple trees. The Grimes Golden, Baldwin, and York Imperial were listed as very susceptible. Many of the symptoms described were similar to those produced by *Phytophthora cactorum*. Orton and Adams found that trees between 7 and 20 years of age were affected, and that the average age of the trees when first infected was between 12 and 13 years, and that on many of the trees the canker was confined to the bark at the base of the trunk, and showed little advancement in a vertical direction.

Phytophthora cactorum causes cankers on the trunks and branches of many kinds of fruit and nut trees. Osterwalder (*30*), in 1912, reported the dying of young grafted apple trees in Switzerland, as a result of a killing of the bark near the graft union by *P. omnivora* de Bary, now considered synonymous with *P. cactorum*. Smith and Smith (*42*), in 1925, described a trunk and crown canker caused by *P. cactorum* and *P. citrophthora* (Smith and Smith) Leonian, on nursery and orchard trees of almond, apricot, cherry, peach, pear, plum, prune, and black walnut in California. A crown and trunk canker of walnut trees in California, caused by *P. cactorum*, was described by Smith and Barrett (*40, 41*) in 1930. Petri (*31*), in 1932, observed mycelium of a *Phytophthora* in the necrotic tissues of apple trees having collar rot, in Italy. In 1934 Curzi (*10*) described a crown rot of peach trees in Italy from which *P. cactorum* was isolated. Dunegan (*12*), in 1935, described a serious canker disease on the stems of young peach seedlings in Arkansas which was caused by *P. cactorum*. In 1938, Lindquist (*25*) described a collar rot of 10-year-old apple trees in Argentina from which *P. cactorum* was isolated. Smith (*39*), in 1937, reported infection on trees and shrubs of 26 plant genera artificially inoculated with a culture of *P. cactorum*. Tucker (*46*) extensively reviewed the literature and showed that *P. cactorum* is rather generally distributed throughout the temperate zones and parasitizes many different hosts. Tucker (*45*) and Smith (*39*) found that cultures of *P. cactorum* were omnivorous.

Tucker (*46*) has adequately reviewed much of the literature dealing with rots of apple and pear fruit caused by *Phytophthora cactorum*. Rose and Lindegren (*34*) obtained infection on uninjured pear and apple fruits placed in dishes containing orchard soil which was covered with water. Cooper (*9*) found that infection of uninjured apple and pear fruits by *P. cactorum* occurred through lenticels, and that zoospores may cause infection. Gardner (*16*) mentioned that apple fruit rot caused by *P. cactorum* occurred year after year in an orchard at Lafayette, Ind., and that the fungus apparently persists in the soil under the trees. Baines (*4, 5*) showed that *P. cactorum*, causing fruit rot, may also cause collar rot, and suggested that the growth of the fungus in the fruit may result in its increase in the soil.

OCCURRENCE OF PHYTOPHTHORA COLLAR ROT IN INDIANA ORCHARDS

During 1933 and 1934, years of severe collar rot epidemics in Indiana, apple trees in seven commercial orchards were examined for collar rot infection with respect to varieties and ages of the trees attacked.

In an orchard at Bedford, and in orchards designated as Nos. 1, 3, and 4 at Vincennes (table 1), an excellent opportunity was afforded

TABLE 1.—*Occurrence of Phytophthora trunk cankers on Grimes Golden in 7 Indiana orchards, in 1933 and 1934*

Location	Age of tree	Trees healthy	Trees affected		
			Less than ½ girdled	½ to completely girdled	Percentage
	Years	*Number*	*Number*	*Number*	
Bedford [1]	13	322	3	23	7.0
	18	28	16	26	60.0
Vincennes:					
Orchard No. 1 [2]	14	58	4	54	50.0
Orchard No. 2	9	300	1	0	.3
	14	141	16	90	43.0
	19	216	5	11	7.0
Orchard No. 3 [3]	11	277	2	1	1.0
	18	49	8	94	68.0
Orchard No. 4 [4]	14	370	175	200	50.0
Bloomfield	16	370	5	92	21.0
Evansville	13	33	0	37	53.0

[1] No infection occurred in this orchard on 58 Delicious and 70 Winesap trees (18 years old), or on 86 Arkansas, 37 Baldwin, 388 Ben Davis, 185 Jonathan, 87 Maiden Blush, 173 Rome Beauty, 46 Stark, 171 Stayman Winesap, 18 Northern Spy, 25 Tompkins King, 8 Willowtwig, and 417 Winesap trees, which were 24 years old.

[2] No infection occurred in this orchard on 1,256 trees 14 years old, of the varieties Jonathan, Oldenburg, Rome Beauty, Stayman Winesap, Yellow Transparent, and York Imperial.

[3] In this orchard of approximately 3,000 11-, 14-, and 18-year-old trees of the varieties Delicious, Grimes Golden, Jonathan, Oldenburg, Rome Beauty, Stayman Winesap, Yellow Transparent, Winesap, and York Imperial, the disease occurred only on Grimes Golden.

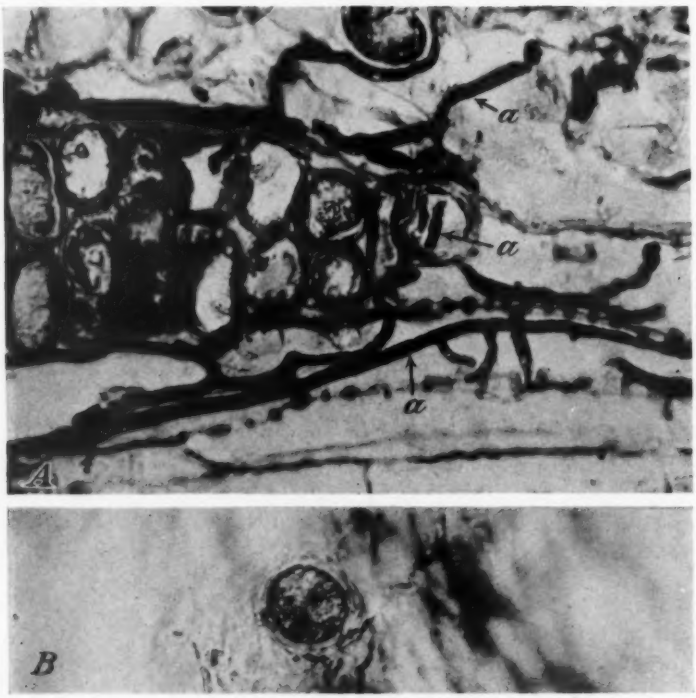
[4] In this orchard, comprised of 220 acres of bearing trees of the varieties Arkansas, Ben Davis, Delicious, Golden Delicious, Grimes Golden, Jonathan, Maiden Blush, Oldenburg, Rome Beauty, Stayman Winesap, Yellow Transparent, Turley, Winesap, Winter Banana, Willowtwig, and York Imperial, infection, other than on Grimes Golden, occurred only on Rome Beauty, and only a few trees of this variety were infected.

to obtain information on the varieties affected, since in many cases other varieties were interplanted among the infected Grimes Golden trees. In these orchards, although Grimes Golden was severely attacked, no collar-rot cankers of a parasitic nature were observed on trees of the following varieties: Arkansas, Baldwin, Ben Davis, Delicious, Golden Delicious, Jonathan, Maiden Blush, Northern Spy, Oldenburg, Stark, Stayman Winesap, Tompkins King, Willowtwig, Winesap, Winter Banana, Yellow Transparent, and York Imperial. Two Rome Beauty trees affected with cankers which girdled the trunks were found in the orchard designated as No. 4 at Vincennes. The cankers appeared similar to those on Grimes Golden.

In six plantings of Grimes Golden trees, 14 to 18 years old, from 21 to 68 percent of the trees were infected with collar rot (table 1). In one planting of 19-year-old Grimes Golden trees 7 percent were infected. Of two plantings of 13-year-old Grimes Golden trees, one was 7 and the other 53 percent infected. Much less infection, 0.3 and 1 percent, occurred on plantings of Grimes Golden trees 9 and 11 years old, respectively. A discussion of this is presented later in connection with the report of inoculation experiments.

SYMPTOMS

Phytophthora cankers occur mainly on the trunks of the trees, but in later stages may involve the bases of the scaffold branches (fig. 1, *C* and *D*). Occasionally, roots near the surface of the ground are invaded. The trunk cankers, frequently irregular in shape, enlarge rapidly in both lateral and vertical directions and may girdle Grimes Golden trees within one season. On double- and high-grafted Grimes



A, Tangential section of infected apple bark showing (*a*) the intercellular and intracellular mycelium of *Phytophthora cactorum; B*, oospore of *P. cactorum* from infected apple bark. × 640.

Golden, the cankers usually do not extend below the graft union, and consequently may not extend to the soil line (fig. 1, *C*). The first symptom of the disease is a wet, discolored area on the surface of the bark, resulting from an exudation of liquid from the killed bark (fig. 1, *A*, *c*). Frequently the cankers are well advanced, and the trunks may be completely girdled before any symptoms are noticeable to a casual observer. In later stages of infection, the bark becomes dry and the cankers are delimited by a definite margin. The bark on old cankers becomes cracked, and may pull away from the trunk (fig. 1, *D*). On severely infected trees the fruit ripens early, the foliage in the fall becomes a reddish-bronze color, and premature defoliation occurs (fig. 2, *A*). The affected trees blossom and leaf out the following spring, after which the leaves and fruit on branches directly above the girdled areas on the trunks usually wilt, and the branches die.

The affected bark of active cankers appears brown and water-soaked, and has a strong, fermented odor. Recently infected bark near the margins of enlarging cankers is light brown in color, with a gradual diminution of the brown color toward the healthy tissues (fig. 1, *B*, *a*). Occasionally, streaks extending 1 to 2 inches beyond the margin of the canker are found near the cambium. Usually the cambium is killed and the sapwood invaded and discolored. The enlargement of the cankers is checked in the fall, presumably by the maturation of the bark tissues. However, cankers which do not girdle trees in one season usually renew activity the following spring at various places on their margins.

PATHOLOGICAL HISTOLOGY

Infected bark from the margins of actively enlarging cankers on the trunks of 13-year-old Grimes Golden trees was fixed, infiltrated with paraffin, and sectioned by the usual method for histological examination. In sections stained in haematoxylin, and aniline blue in picric acid, the mycelium of the fungus, which stained blue, was readily differentiated from the host tissues. An abundance of both intercellular and intracellular coenocytic mycelium was observed in all parts of the infected bark (pl. 1, *A*, *a*). The infection caused a distinct disorganization of the host-cell protoplast and a break-down of the cell walls, especially of the parenchyma. Mycelium was not observed in advance of the discolored area of affected tissues.

Numerous oospores or chlamydospores, apparently those of *Phytophthora cactorum*, were found in mascerated bark collected in the spring from an overwintering canker produced by artificial inoculation (pl. 1, *B*). No sporangial stage of the fungus on the surface of the cankers was found by macroscopic examination of many cankers.

INFECTIOUS NATURE OF CANKER TISSUE

Early in the investigations, this type of collar rot was demonstrated to be infectious when cankers resulted from inoculations made by inserting pieces of infected bark into the trunks of five healthy Grimes Golden trees 13 years old. Inoculations were made with bark taken from each of five cankers. The inoculations were covered with cheesecloth and grafting wax. Typical cankers, from 5 to 15 cm. in diameter, resulted after 2 weeks from inoculations made with bark from four cankers.

FIGURE 1.—*Phytophthora cactorum* cankers on Grimes Golden trees: *A*, Canker (*a*) on an 11-year-old tree 2 months after inoculation at *b*. The moist dark-colored area (*c*) is the first exterior symptom of the disease. *B*, The same canker as in *A* with the outer bark removed at *a* to show the light-brown, advancing margin of the canker. *C*, Trunk of tree illustrated in Figure 2,*A*. The canker (*a*) was confined to the trunk and bases of the main branches and did not invade the stock (*b*). The graft union (*c*) sharply limited the canker to the Grimes Golden tissues. Healthy light-colored tissue at the margin of the canker has been exposed by removal of the outer bark. *D*, Trunk of a 14-year-old tree girdled by an old canker with infected bark dry, cracked, and invaded by other organisms. The canker did not advance appreciably above the bases of the main branches at *a*, *b*, and *c*, nor infect the inarch (*d*) at the side of the trunk.

FIGURE 2.—*A*, 14-year-old, high-grafted Grimes Golden tree with trunk above the graft union (*a*) girdled by *Phytophthora cactorum* (see fig. 1, *C*). The tree was distinguished by the yellowish-green foliage, becoming redd sh at the tips of the upper branches (*b*, *c*, and *d*), and by the partial defoliation. *B*, 14-year-old Grimes Golden trees (*a*, *b*, and *c*) girdled by *P. cactorum* and pulled up. The roots of 50 similar trees examined, except 1, were healthy.

RELATION OF BACTERIA TO THE DISEASE

Numerous bacterial colonies were obtained from infected bark of 17 trunk cankers of Grimes Golden trees by the dilution-plate method. Bacteria from these cankers were nonpathogenic when inoculated into 14- and 18-year-old Grimes Golden tree trunks, Briarcliff and Premier rose shoots, Rome Beauty and Winesap apple shoots, and Bartlett pear fruits.

Although pathogenic bacteria were not isolated from trunk cankers of Grimes Golden, inoculations were made on this variety with the fire blight organism, *Erwinia amylovora*, in an attempt to produce cankers typical of the collar rot disease. Three cankers less than 3 cm. in diameter, and delimited by cork at their margins, resulted from 12 inoculations made on the trunks of 11 14-year-old and 1 18-year-old Grimes Golden trees on May 11, 1934. Five bark cankers similar to these were also formed around the bases of inoculated succulent shoots which were on the trunks or bases of the first main branches of these trees. The culture of *E. amylovora* used in the inoculations was pathogenic on apple shoots and pear fruits. Obviously the trunk canker disease of Grimes Golden differed greatly from that caused by fire blight.

THE CAUSAL FUNGUS (PHYTOPHTHORA CACTORUM)

ISOLATION

Phytophthora cactorum [7] was consistently isolated from small pieces of infected bark taken from the margins of enlarging cankers. The infected bark tissue was surface-sterilized in a solution of 1:1,000 mercuric chloride, twice rinsed in sterile water, and then plated on potato-dextrose agar. Other fungi, including an undetermined species of *Alternaria*, and a few bacteria, grew from some of the tissue plantings. No infection was obtained when the alternaria fungus was inoculated into the bark of the trunk of an 18-year-old Grimes Golden tree. The bacteria which grew from some of the plantings were not typical of *Erwinia amylovora*, and apparently were similar to those obtained by the dilution-plate method mentioned earlier.

During 1934–36, *Phytophthora cactorum* was obtained from 49 of the 64 cankers on the trunks of Grimes Golden trees from which isolation was attempted. The cankers from which the fungus was isolated were collected in 11 orchards in the vicinity of Bedford, Bloomfield, Evansville, Indianapolis, Mitchell, and Vincennes, Ind. All colonies of *P. cactorum* obtained from the 49 cankers, except 1, appeared to be similar in cultural characters on potato 2-percent dextrose agar. From 1 canker both an atypical culture and a typical culture of *P. cactorum* were isolated.

The isolation of *Phytophthora cactorum* from inactive cankers was found difficult by the tissue-planting procedure. However, when apple fruits were inoculated with small pieces of infected bark from the margins of such cankers, a rot frequently developed from which *P cactorum* was readily isolated. The percentage of inoculations of this type producing infection of the fruits was rather low when the bark was secured from the centers of cankers.

[7] The writer gratefully acknowledges the assistance of Dr. C. M. Tucker in the identification of the culture.

Fallen apples on the ground were frequently found rotted by *Phytophthora cactorum* during 1934–36. Cultures of *P. cactorum*, which appeared similar to those obtained from cankers, were obtained from 46 Grimes Golden, 5 Baldwin, 2 Stayman Winesap, and 3 Thompkins King fruits.

Phytophthora cactorum was also isolated from orchard soil. Twenty-eight samples of surface soil were collected in five orchards on October 15, 1935, and 7 and 11 samples were collected in an orchard at Lafayette on September 29 and October 24, 1936, respectively. The soil from each sample was introduced into shallow holes made in Grimes Golden fruits that had been picked at a height of 4 to 6 feet and washed in 95-percent alcohol. The soil was sealed in with petroleum jelly, and the inoculated apples were placed in waxed paper bags to retard drying, and incubated at 24° C. After 9 days decay was evident around many of the inoculations, and tissue plantings were made from the rots more or less typical of *P. cactorum*.

No cultures of *Phytophthora cactorum* were isolated from the fruits inoculated with soil collected on October 15, 1935. Cultures were obtained from 2 of the 7 samples of soil collected on September 29, 1936, and from 1 of the 11 samples collected on October 24, 1936. From many of the inoculations a soft rot developed which was not typical of *P. cactorum*. No decay developed on 12 fruits which were punctured with a cork borer, nor on 4 into which sterile soil was introduced.

PATHOGENICITY

Material and Methods

To test the pathogenicity of *Phytophthora cactorum* on Grimes Golden trees, 12 cultures were selected as being representative of the cultures in type of growth on potato-dextrose agar. Of the cultures selected, Nos. 1 to 7 (table 2) were isolated from cankers on the trunks of Grimes Golden trees at Bedford, Evansville, and Vincennes; Nos. 9 to 11 from apple fruits at Lafayette and Vincennes; and Nos. 26 and 27 from soil at Lafayette. The pathogenicity of culture 1 also was tested on trees of two additional species of apple, on two species of cherry, on three of plum, and on one of peach, pear, and quince which were growing in a field plot.

Inoculations were made with these cultures on 140 Grimes Golden apple trees, 2 to 30 years old, during 1934–38. All the trees inoculated, unless otherwise stated, were growing normally. Nearly all the inoculations were made during June, July, and August. The trees were inoculated by inserting a small quantity of mycelium and agar into a deep incision made with the point of a scalpel. The inoculum was obtained from colonies 3 to 5 days old grown on potato 2-percent dextrose agar. The inoculations were covered with cheesecloth and sealed with warm, low melting point grafting wax (fig. 3, *A*). Before each inoculation the instruments used were flamed. During 1934 the check incisions were made similarly to the above, except that no inoculum was introduced into the wound. However, in 1935–36 a small quantity of sterile potato-dextrose agar was inserted in the check incisions.

Results of Inoculations

All the cultures except No. 2 (table 2) were severely pathogenic on the trunks of Grimes Golden trees between 8 and 30 years of age

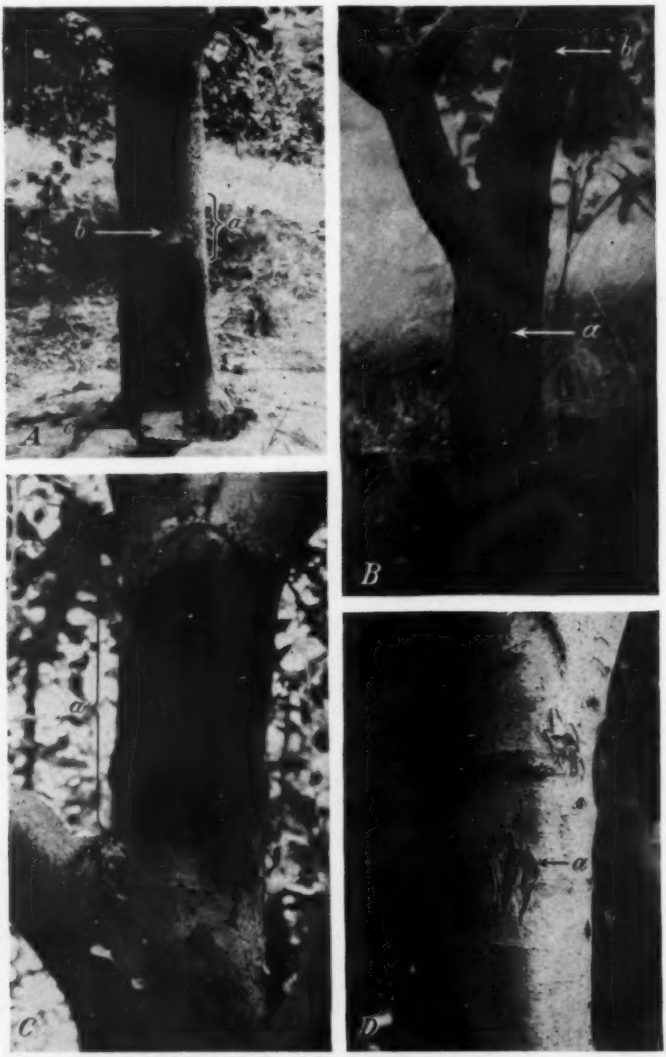


FIGURE 3.—*A*, Infection (*a*) not externally visible on trunk of a 13-year-old Grimes Golden tree 3 weeks after inoculation at (*b*). The wet, discolored area below the canker caused by exudation of a liquid from the infected area is the first external symptom of the disease. No infection resulted from an inoculation (*c*) on the Virginia crab stock. *B*, Inoculation incision (*a*) on a resistant (Jonathan) variety, with outer bark cut away to show the sharp limitation of the disease; check incision (*b*) on branch, which was similar to that on the trunk. *C*, Canker (*a*) produced by artificial inoculation on Grimes Golden branch 15 cm. in diameter. *D*, Slight enlargement at (*a*) of an inoculation incision, which had ceased enlarging and was classified as infection failure, on a Grimes Golden branch 8 cm. in diameter.

Cultures Nos. 1, 3 to 7, 9 to 11, 26, and 27 were severely pathogenic on trees 8 or more years old. Usually the cankers were 20 to 25 cm. in diameter 1 month after inoculation, and showed no evidence of being checked (fig. 1, *A*, *B*). In many cases the cankers girdled the 11- to 14-year-old Grimes trees within 3 months after inoculation. *Phytophthora cactorum* was obtained from each of the 32 cankers from which reisolation was attempted. No infection occurred on the 2- to 4-year-old trees, which were inoculated with culture No. 1.

A canker resulted from only one of five inoculations made with culture No. 2, although it was isolated from a canker and was similar in culture to the highly parasitic strains. This canker increased rapidly in size, suggesting that with this culture infection is established with difficulty, although it is capable of developing once established.

TABLE 2.—*Pathogenicity of* Phytophthora cactorum *on Grimes Golden trees in Indiana orchards*

Source of culture	Culture No.	Year of inoculation	Age of trees	Trees inoculated	Inoculations [1]	
					Total	Producing cankers [2]
			Years	*Number*	*Number*	*Number*
Canker	1	1935	2	5	8	0
Do	1	1936	3	5	8	0
Do	1	1937	4	5	8	0
Do	1	1938	5	3	6	1
Do	1	1935	8	3	3	3
Do	1	1934	11	1	2	2
Do	1	1936	11	12	15	13
Do	1	1935	12	4	4	4
Do	1	1934	13	12	14	13
Do	1	1935	14	33	33	25
Do	1	1934	18	2	8	8
Do	1	1935	19	6	13	12
Do	1	1935	20	28	29	27
Do	1	1935	30	2	6	5
Do	2	1935	19	2	5	1
Do	3	1936	11	1	2	2
Do	3	1935	19	2	5	5
Do	4	1935	19	2	5	3
Do	5	1935	19	2	5	5
Do	6	1935	19	2	5	4
Do	7	1935	19	2	5	5
Fruit rot	9	1935	19	2	5	4
Do	10	1936	11	1	2	1
Do	11	1935	19	2	5	4
Soil	26	1936	11	2	4	3
Do	27	1936	11	2	4	2

[1] No cankers resulted from the 113 check incisions.
[2] *P. cactorum* was obtained from each of 32 cankers from which reisolation was attempted.

The results of inoculation of the trunks of species of *Prunus*, *Pyrus*, and *Cydonia* with culture No. 1 of *Phytophthora cactorum* are presented in table 3. Two-year-old trees of *Prunus mahaleb* L. (cherry), *P. avium* L. (cherry), *P. americana* Marsh. (plum), and 6-year-old trees of *P. persica* (L.) Batsch. var. Elberta (peach), and 1 tree of *P. domestica* L. var. Reine Claude (plum), 20 years or more old, were highly susceptible to infection by *P. cactorum* (fig. 4, *A*, *B*, *C*). Only one of five 2-year-old trees of *Prunus cerasifera* Ehrh. (plum) became infected. No infection occurred on 2-year-old trees of *Pyrus baccata* L. (apple), *P. coronaria* L. (apple), *P. serotina* Rehd. (pear), and *Cydonia oblonga* Mill. (quince).

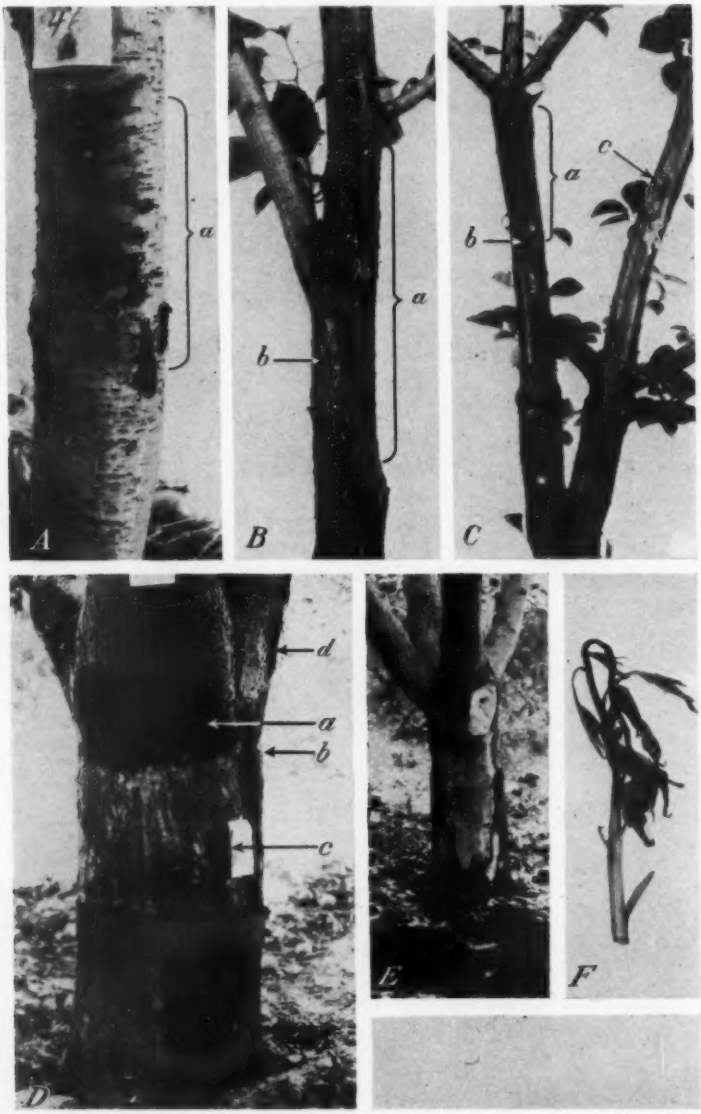


FIGURE 4.—*A*, Canker (*a*) on 6-year-old peach tree (artificial inoculation). *B*, Canker (*a*) on 2-year-old mazzard cherry tree resulting from inoculation at *b*. *C*, Canker (*a*) on 2-year-old mahaleb cherry tree resulting from inoculation at *b*; check incision at *c*. *D*, Inoculations on 20-year-old, double-worked Grimes Golden tree producing canker (*a*) on Grimes scion, which extended to graft union (*b*), but no infection from inoculation on Delicious stock (*c*), nor from check incision (*d*) on Grimes scion. *E*, Canker on trunk of 14-year-old Grimes Golden tree treated by scarification and ready for painting with Bordeaux paint. *F*, Infection of peony shoot following artificial inoculation with a virulent culture.

TABLE 3.—*Results of inoculation of trees of Prunus, Pyrus, and Cydonia species with culture No. 1 of Phytophthora cactorum*

Species	Age of tree	Trunks inoculated	Cankers produced [1]	Check incisions [2]
	Years	*Number*	*Number*	*Number*
Prunus avium	2	5	3	5
Prunus mahaleb	2	5	5	5
Prunus americana	2	5	4	5
Prunus cerasifera	2	5	1	5
Prunus domestica	20	[3] 4	2	0
Prunus persica	6	3	3	3
Pyrus baccata	2	5	0	5
Pyrus coronaria	2	5	0	5
Pyrus serotina	2	5	0	5
Cydonia oblonga	2	5	0	5

[1] Apparently pure cultures of *Phytophthora cactorum* were reisolated from cankers on *Prunus avium*, *P. mahaleb*, *P. americana*, and *P. domestica*.
[2] No infection resulted from the check incisions.
[3] Inoculations made on large branches.

No infection resulted from the check incisions during these tests. This fact was considered to justify the practice of not sterilizing the surface of the bark prior to inoculating. The orchards in which the inoculations were made were relatively free from fire-blight and collar-rot infection.

PHYSIOLOGIC SPECIALIZATION

MATERIAL AND METHODS

The inoculations to differentiate physiologic races of the fungus, unless otherwise stated, were made in a 10-year-old orchard of Grimes Golden trees, which contained 1 or 2 trees of each of the 30 other varieties listed in table 5 and footnote 2 of that table. These trees appeared normal, and a week before they were inoculated in July 1936, between 300 and 400 gallons of water were applied under each tree to insure plentiful soil moisture during the experiment. The sources of the 12 cultures of *Phytophthora cactorum* tested are given in table 4. Inoculations were made on the trunk of each tree, except Grimes Golden, with the 10 cultures Nos. 1, 8, and 12 to 19. Each of the 12 cultures was tested on one or more Grimes Golden trees. One check incision on each tree, into which sterile potato-dextrose agar was introduced, remained free from infection during these tests. The inoculations were made as previously described. In addition, inoculations with culture No. 1 were made on 28 varieties, between 12 and 30 years old (footnote 3, table 5). The number of trees available for inoculation was limited because of the danger of killing valuable trees of bearing age.

TABLE 4.—*Cultures of Phytophthora cactorum tested for physiologic specialization*

Culture No.	Host	Place isolated and year	Collector or source of culture [1]
1	Grimes Golden apple tree	Indiana, 1934	Writer.
8	do	do	Do.
12	Apple fruit		Baarn, Netherlands.
13	*Lilium candidum*	Indiana, 1936	E. P. Imle.
14	Lilac	Massachusetts, 1929	K. S. Chester.
15	Peony	Indiana	Baarn, Netherlands.
16	Citrus	Korea	Do.
17	*Eriobotrya japonica*	Japan	T. Tasugi.
18	Snapdragon	California, 1932	M. P. Harris.
19	*Pinus* sp.		Baarn, Netherlands.
20	Unknown		Do.
21	*Lilium dauricum*	Japan	T. Tasugi.

[1] Cultures Nos. 12 and 14 to 21, inclusive, were received from C. M. Tucker.

TABLE 5.—*Pathogenicity and physiologic specialization of cultures of Phytophthora cactorum described in table 4 on 10-year-old appletrees, and on flax and peony plants*

Culture No.[1]	Source of culture	Virulence of cultures on 7 apple varieties and on flax and peony [2]								
		Gano	Grimes Golden	Tompkins King	Northwestern Greening	Rome Beauty	Smokehouse	Stark	Flax	Peony
[3] 1	Grimes Golden trees	0(2)	3(3); 0(3)	3(1); 0(1)	3(1)	3(1); 0(1)	0(1)	3(1); 0(1)	1(4); 0(6)	3(13); 2(2)
8	do	3(1); 0(1)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	2(1); 1(9)	3(13); 2(2)
12	Apple fruit	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	1(6); 0(4)	3(15)
13	Lily	0(2)	0(6)	3(2)	0(1)	3(1); 0(1)	0(1)	3(1); 0(1)	3(2); 1(6); 0(2)	3(7); 2(6); 1(2)
14	Lilac	0(2)	[4] 0(5)	3(1); 0(1)	0(1)	0(2)	0(1)	0(2)	1(2); 0(8)	3(1); 2(3); 1(6); 0(5)
15	Peony	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(1); 1(7); 0(2)	0(15)
16	Citrus	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(5); 0(5)	2(4); 1(7); 0(4)
17	Loquat	0(2)	0(6)	3(1); 0(1)	0(1)	0(2)	3(1)	0(2)	3(1); 1(4); 0(5)	3(10); 2(4); 1(1)
18	Snapdragon	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(9); 1(1)	3(5); 2(10)
19	Pine	0(2)	0(6)	0(2)	0(1)	0(2)	0(1)	0(2)	3(6); 1(4)	3(9); 2(4); 0(2)
20	Unknown	----------	0(6)	----------	----------	----------	----------	----------	3(10)	3(15)
21	Lily	----------	0(6)	----------	----------	----------	----------	----------	3(5); 1(5)	3(15)

[1] No infection resulted from inoculations made with cultures Nos. 1 and 8 to 19, inclusive, on the following 10-year-old trees not included in the table: 1 Arkansas, 2 Baldwin, 2 Ben Davis, 2 Cortland, 2 Delicious, 1 Early Harvest, 2 Golden Delicious, 1 Hubbardston, 1 King David, 1 Lowland Raspberry, 2 McIntosh, 1 Maiden Blush, 1 Northern Spy, 1 Oldenburg, 1 Paragon, 1 Rhode Island Greening, 2 Stayman Winesap, 2 Starking, 1 Wagener, 2 Wealthy, 2 Winesap, 1 Winter Banana, 2 Yellow Transparent, and 1 York Imperial.

[2] Virulence of the cultures is designated by numerals as follows: Nonpathogenic, 0; slightly virulent, 1; moderately virulent, 2; and extremely virulent, 3. First numeral indicates virulence, and number in parenthesis following virulence figure indicate number of trees or plants so affected.

[3] Culture No. 1 was also tested on 28 varieties of apple trees from 12 to 30 years old and not reported in the table. Infection resulted on 5 Northwestern Greening and on 1 of the 3 Rome Beauty trees inoculated. No infection resulted on 10 Arkansas, 1 Baldwin, 2 Benoni, 6 Ben Davis, 14 Delicious, 4 Fameuse, 3 Hibernal, 2 Hubbardston, 5 Jonathan, 7 Lowland Raspberry, 5 McIntosh, 2 Maiden Blush, 1 Mann, 7 Northern Spy, 8 Oldenburg, 3 Red Astrachan, 1 Rhode Island Greening, 5 Stayman Winesap, 1 Tompkins King, 4 Transcendent crab, 2 Virginia crab, 5 Walbridge, 2 Wagener, 9 Wealthy, 8 Winesap, and 1 Winter Banana. No infection resulted from inoculations in which culture No. 1 was used on the trunks of 2-, 3-, and 4-year-old trees of the following varieties: Benoni, Black Ben, Delicious, Golden Delicious, Golden Sweet, Jonathan, Maiden Blush, McIntosh, Oldenburg, Romè Beauty, Red Rome, Red Delicious, Stayman Winesap, Turley, Wealthy, Winesap, Yellow Transparent, and York Imperial. Four trees of each variety were inoculated twice during 3 consecutive years.

[4] No infection resulted from 5 inoculations on 5 10-year-old trees; 3 cankers resulted from 5 inoculations on 2 19-year-old trees.

Three-week-old flax (Red Wing) plants and peony (Mme. Boulanger) shoots growing in a greenhouse also were inoculated with the 12 cultures of *Phytophthora cactorum* listed in table 4. A small quantity of mycelium from a culture on pototo-dextrose agar was inserted in the stems and covered with a piece of rubber tape. Two groups of 5 plants of flax were grown separately in a greenhouse bench and inoculated with each culture. The tests on peony were conducted in two trials. Five shoots were inoculated in the first trial and 10 in the second. A similar number of check plants treated with sterile potato-dextrose agar instead of inoculum remained free from infection during these tests.

The virulence of the cultures on flax and peony was recorded by assigning values of 0, 1, 2, and 3 to the recognized classes of infection resulting from the inoculations. The value 3 was assigned to the severely infected plants, 0 to the plants not infected, and intermediate values to the plants in the intermediate classes. A virulence of 3 was assigned to the cultures which were pathogenic on the 10-year-old apple trees.

Differential Pathogenicity of Cultures

Culture No. 1 isolated from a Grimes Golden trunk was the most widely pathogenic culture on the apple varieties, producing cankers on Grimes Golden, Tompkins King, Northwestern Greening, Rome Beauty, and Stark (table 5). Four other cultures also produced cankers on apple trunks, but differed from culture No. 1 and from one another in the varieties that they infected. Culture 13, from *Lilium candidum* L., was pathogenic on Tompkins King, Rome Beauty, and Stark. Culture 17, from loquat, infected Tompkins King and Smokehouse, being the only culture to infect the latter variety. Culture 14, from lilac, infected only Tompkins King of the 10-year-old trees, but it also infected 19-year-old Grimes Golden in another test. Culture 8, isolated from a Grimes Golden trunk and atypical in growth on media, infected only Gano, and was the only culture to infect this variety. Cultures Nos. 12, 15, 16, 18, and 19 failed to infect any of the above-mentioned seven varieties, which were infected by one or more of the other cultures. Cultures 20 and 21 were nonpathogenic on Grimes Golden. *Phytophthora cactorum* was reisolated from cankers formed by the pathogenic cultures.

Inoculations of flax and peony also brought out differences in pathogenicity of the cultures. Cultures 1, 8, 13, 14, and 17, pathogenic on one or more varieties of apple, were only slightly pathogenic on flax. With the exception of cultures 12 and 15, all of the remaining cultures that were nonpathogenic on apple were highly virulent on flax. All the cultures except No. 15, were highly virulent on peony (fig. 4, *F*). *Phytophthora cactorum* was reisolated from infected flax and peony plants.

The data presented above are too limited to permit definite classification of races of *Phytophthora cactorum*. However, the writer believes that significant differences in the capacity of cultures of *P. cactorum* to cause collar rot on different apple varieties have been demonstrated.

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VARIETAL SUSCEPTIBILITY

TRUNK CANKER

Seven apple varieties were susceptible to phytophthora trunk canker (table 5). The Gano variety was infected by one culture, Grimes Golden by two, Tompkins King by four, Northwestern Greening by one, Rome Beauty by two, Smokehouse by one, and Stark by two. A culture of *Phytophthora cactorum* isolated from peony in 1937, and not included in table 5, was pathogenic on the trunks of 20-year-old Grimes Golden.

No infection resulted on trunks of 10-year-old Arkansas, Baldwin, Ben Davis, Winter Banana, Cortland, Delicious, Oldenburg, Early Harvest, Golden Delicious, Hubbardston, King David, Lowland Raspberry, McIntosh, Maiden Blush, Northern Spy, Paragon, Rhode Island Greening, Stayman Winesap, Starking, Wagener, Wealthy, Winesap, Yellow Transparent, and York Imperial apple trees when inoculated with cultures 1, 8, and 12 to 19. In addition, Benoni, Fameuse, Hibernal, Mann, Red Astrachan, Transcendent crab, Virginia crab, and Walbridge apple trees, 13 to 30 years of age, were resistant to infection by culture No. 1. The inoculations on the trunks from which no infection was recorded, in many cases developed a slight enlargement of the inoculation incision (fig. 3, *B*). In some cases, only one or two inoculations were made with a given culture on a variety. Therefore, final conclusions on the reaction of a variety to a given culture cannot be made from these tests.

ROOT ROT

Cankers near the bases of the trunks of an own-rooted Grimes Golden, 14 years old, and of an 18-year-old Grimes Golden on French crab seedling roots, extended into the large roots. The writer was unable to determine whether the infected roots arose from the Grimes Golden scion of the latter tree. Apparently pure cultures of *Phytophthora cactorum* were isolated from diseased bark from the roots of both trees. The cankers on the roots had definite margins and the infected periderm was brown and soft. In an orchard at Vincennes, 14-year-old Grimes Golden trees severely girdled by phytophthora trunk cankers were pulled with a tractor (fig. 2, *B*). The French crab seedling roots of 49 of these trees were healthy. On 1 tree a large root was decayed by an undetermined organism.

FRUIT ROT

Apple fruits of 29 varieties were inoculated with *Phytophthora cactorum* culture No. 1. Two fruits of each variety were taken from cold storage on November 29, 1935, swabbed with 95-percent alcohol, and inoculated by introducing into a puncture a small quantity of mycelium from a young culture. The inoculations were sealed with petroleum jelly. A check puncture was made on the side of each fruit opposite the inoculation. Each variety was enclosed in a waxed paper bag.

Typical decay was produced by all the inoculations and none by the check punctures. After 1 week the infected areas were between 3.3 and 6.3 cm. in diameter on the Baldwin, Ben Davis, Oldenburg, Fameuse, Grimes Golden, Hubbardston, Jonathan, Tompkins King,

Lowland Raspberry, McIntosh, Maiden Blush, Northern Spy, Northwestern Greening, Rome Beauty, Gallia Beauty, Red Delicious, Rhode Island Greening, Stark, Stayman Winesap, Smokehouse, Yellow Transparent, Turley, Wagener, Winesap, Winter Banana, and York Imperial varieties, between 2.2 and 3.3 cm. on Banks and Golden Delicious, and 1.3 cm. on Arkansas.

FACTORS AFFECTING RESISTANCE AND SUSCEPTIBILITY TO COLLAR ROT

RELATION OF AGE AND VIGOR OF GRIMES GOLDEN TREES TO INFECTION

The trunks of Grimes Golden trees ranging in age from 2 to 30 years were inoculated with culture No. 1 (table 2). The 2-year-old trees were nursery-budded and were inoculated the season that they were replanted. These young trees grew vigorously, and were reinoculated twice during each of the following 3 years. No infection occurred until the fourth year. Then one canker resulted from six inoculations on three 5-year-old trees. The marked resistance of the 2- to 4-year-old trees is difficult to explain. Presumably a similar type of resistance occurred when large scaffold branches of older trees were inoculated, as will be shown later. Typical cankers were produced on the trunks of Grimes Golden trees 8 to 30 years old. All the trees were growing well when inoculated, except two 30-year-old trees and a few 14-year-old trees on poor soil. Typical cankers were obtained on the 30-year-old trees, but the small, slow-growing 14-year-old trees on areas of poor soil appeared to be more resistant to infecton than more vigorous trees in the same orchard.

Under conditions of natural infection the disease occurs chiefly on Grimes Golden trees over 13 years of age, as mentioned above. However, Grimes Golden trees 8 and 11 to 13 years of age were easily infected when mycelium of the fungus was introduced into the bark of the trunks. It appeared likely that these younger trees escape infection through the operation of some factors other than internal resistance to the parasite. Therefore, a series of inoculations was made by placing inoculum on the uninjured bark of 11- and 19-year-old trees. Colonies of culture No. 1, grown for 2 weeks on prune-extract medium, were placed on the uninjured surfaces of the trunks of Grimes Golden trees, and covered with moist cheesecloth and heavy wrapping paper for 3 days. Check areas were treated similarly, except that no inoculum was used. From nine inoculations made on six, 19-year-old trees, six cankers developed on four trees. One month after inoculation the cankers were 13 to 25 cm. in diameter and showed no evidence of being checked. The fungus was reisolated from four cankers. No infection resulted from four inoculations and two check treatments made on six 11-year-old trees nor from five check treatments on 19-year-old trees. The results show 19-year-old trees to be susceptible to infection from inoculum placed on the unwounded trunk, and they suggest a structural resistance in 11-year-old trees to infection from such inoculation.

RESISTANCE OF BRANCHES

Cankers caused by natural infection with *Phytophthora cactorum* have never been observed by the writer on scaffold branches. To

determine whether the branches are actually resistant or whether they merely escape infection, inoculations were made during 1935 on both the trunks and branches of 22 varieties ranging in age from 12 to 30 years. Mycelium of culture No. 1 of *P. cactorum* was placed in incisions in the bark, as previously described.

Typical cankers resulted on the trunks of 38 of 46 Grimes Golden trees inoculated (table 6). However, only 3 cankers developed from 70 inoculations on branches. One canker, 20 cm. long, encircled a branch 5 cm. in diameter on a 12-year-old Grimes Golden. The canker was sunken, had a definite margin, and the cambium under most of the canker appeared healthy. *Phytophthora cactorum* was reisolated. A second branch canker, 7 cm. in diameter, occurred on a branch 8 cm. in diameter on a 14-year-old Grimes Golden tree. It was definitely checked in growth and delimited from sound bark. A third canker occurred on a main scaffold branch 15 cm. in diameter on a 19-year-old tree. Two months after inoculation the canker was 35 cm. in diameter and still enlarging (fig. 3, *C*). No infection occurred on the trunks or branches of the other 21 varieties inoculated except Rome Beauty. A trunk canker resulted from inoculations on 2 Rome Beauty trees. From all the inoculations of branches that were classed as no infection, a slight enlargement of the inoculation wound took place (fig. 3, *D*).

TABLE 6.—*Susceptibility of the branches and trunks of apple trees to infection by Phytophthora cactorum, culture No. 1*

Variety [1]	Age of trees	Trees inoculated	Trunks infected [2]	Inoculations on branches		
				Diameter of branches inoculated	Inoculations	Cankers produced
	Years	*Number*	*Number*	*Centimeters*	*Number*	*Number*
Grimes Golden	12	4	4	5–7	4	1
	13	4	4	4–7	4	0
	14	33	25	5–10	33	1
	19	2	2	7–15	7	1
	19	1	1	2–15	18	0
	20	1	1	11	1	0
	30	1	1	10	3	0
Rome Beauty	13	1	1	5–7	2	0
	30	1	0	12	2	0

[1] No infection resulted from a trunk and branch inoculation on 4 Arkansas, 1 Winter Banana, 2 Baldwin, 1 Benoni, 3 Oldenburg, 6 Fameuse, 3 Hibernal, 2 Hubbardston, 4 Jonathan, 2 Tompkins King, 10 McIntosh, 2 Maiden Blush, 1 Mann, 2 Northern Spy, 1 Rhode Island Greening, 2 Red Astrachan, 5 Stayman Winesap, 2 Wagener, 9 Wealthy, and 8 Winesap trees, 12 to 30 years of age.

[2] No infection resulted from 44 check incisions in the trunks.

INTERACTION OF STOCK AND SCION COMPONENTS OF GRAFTED TREES IN RELATION TO RESISTANCE AND SUSCEPTIBILITY

In an effort to avoid trunk cankers, Grimes Golden trees are frequently propagated by grafting the Grimes scion on the stock, 6 or more inches above the soil line, and also by double-working, i. e., by using a second variety to form the base of the trunk onto which the Grimes Golden is grafted. Such trees were used to study the possible effect of stock-scion interaction on the respective susceptibility or resistance of the component parts of the trees to infection by *Phytophthora cactorum*. Fourteen- and twenty-year-old Grimes Golden trees propagated on 13 varieties of stocks, were available for this

test. The Grimes Golden trees, propagated on 5 varieties, had been double-worked in the nursery. The roots of these trees were French crab seedlings. The Grimes Golden scions on 8 varieties of own-rooted stocks had been grafted 8 to 18 inches above the soil line. The roots of the own-rooted stocks were of the same variety as the base of the trunk. Inoculations were made with culture No. 1 near the graft union on the Grimes Golden and also on the stock variety of each tree (fig. 4, *D*).

Large trunk-cankers were formed on the scion, or Grimes Golden portion, of 56 of the 68 trees inoculated (table 7). Northwestern Greening was the only variety of stock tested that was susceptible, cankers resulting from four of the six inoculations made on four, 20-year-old double-worked trees. No infection occurred from the inoculations on stocks of the varieties Arkansas, Red Astrachan, Delicious, Oldenburg, Fameuse, Hibernal, Lowland Raspberry, Northern Spy, Northern Spy seedling, Transcendent crab, Walbridge, and Wealthy, nor from the check incisions. The downward advance of the cankers on the Grimes Golden bark was checked at the graft union with the resistant stocks. However, when the Grimes Golden was on Northwestern Greening stock, the cankers extended across the graft unions. In this experiment there appeared to be no interaction between the stock and scion which influenced the characteristic resistance or susceptibility of the varieties.

TABLE 7.—*Results of inoculations of stock and scion components of the trunks of high- and double-grafted Grimes Golden trees with culture No. 1 of Phytophthora cactorum*

Varietal composition of the trees [1]		Age of trees	Trees inoculated	Component varieties of trunks inoculated	Inoculations [2]	Cankers produced
Intermediate stock	Rootstock					
		Years	*Number*		*Number*	*Number*
Arkansas	French crab seedling	20	8	Grimes Golden	8	7
				Arkansas	8	0
None	Red Astrachan	14	1	Grimes Golden	1	1
				Red Astrachan	1	0
Delicious	French crab seedling	14	6	Grimes Golden	6	4
				Delicious	5	0
Do	do	20	10	Grimes Golden	10	9
				Delicious	9	0
None	Oldenburg	14	6	Grimes Golden	6	3
				Oldenburg	7	0
Do	Fameuse	14	1	Grimes Golden	1	1
				Fameuse	1	0
Do	Hibernal	14	3	Grimes Golden	3	3
				Hibernal	3	0
Do	Lowland Raspberry	14	6	Grimes Golden	6	5
				Lowland Raspberry	6	0
Northwestern Greening	French crab seedling	20	4	Grimes Golden	4	4
				Northwestern Greening	6	4
None	Northern Spy	14	4	Grimes Golden	4	2
				Northern Spy	4	0
Do	Northern Spy seedling	14	3	Grimes Golden	2	2
				Northern Spy seedling	3	0
Do	Transcendent crab	14	4	Grimes Golden	4	3
				Transcendent crab	4	0
Walbridge	French crab seedling	20	5	Grimes Golden	5	4
				Walbridge	5	0
None	Wealthy	14	6	Grimes Golden	6	6
				Wealthy	6	0
Do	Grimes Golden	14	1	Grimes Golden	2	2

[1] Scion always Grimes Golden

[2] No cankers resulted from 64 check incisions in trunks of Grimes Golden and 2 in trunks of the Arkansas variety.

CONTROL OF THE DISEASE

EFFECT OF HEIGHT OF THE GRAFT UNION ON INFECTION

During 1933 and 1934 collar rot of Grimes Golden appeared to be more prevalent on low-grafted and budded trees than on double-worked trees. Therefore, measurements were made of the height of the graft unions formed between the Grimes scion and the stock, to determine whether collar-rot cankers were more prevalent on trees with low than with high graft unions. These measurements were made in an orchard of 467 double-worked, 16-year-old trees in which 21 percent were killed by phytophthora collar rot.

The height of the graft unions of the diseased and the healthy trees ranged respectively, from 0 to 22 and from 0 to 24 inches above the soil. The mean height of the graft unions of trunk canker-infected trees was 12.4 inches and that of uninfected trees 12.8 inches. Of 354 trees with graft unions 15 inches or less above the soil, 75, or 21 percent, were infected. Of the remaining 113 trees with higher graft unions, 22, or 19 percent, were infected. Within a group of 15 trees having graft unions 20 to 24 inches above the soil 7 were infected. Evidently the propagation of Grimes Golden trees by grafting 15 to 22 inches above the soil is not effective in reducing natural infection with *Phytophthora cactorum*.

Apple growers interviewed, however, are of the opinion that in general less infection occurs on double-worked trees than on regular grafted and budded trees. It may be that in years when phytophthora collar-rot does not occur in epidemic severity, double-worked trees are not so readily infected as low-grafted and budded trees. The use of resistant varieties of apple to form the roots and trunk of the trees, and the grafting of the Grimes Golden variety on these stocks 30 inches or more above the soil, may still be a means of reducing infection from *Phytophthora cactorum*, although no observations have been made of Grimes Golden trees grafted at this height.

BORDEAUX MIXTURE AS A PREVENTATIVE OF COLLAR ROT

The effectiveness of bordeaux mixture as a preventive of collar rot was tested in two orchards. A 16:16:100 bordeaux mixture containing 1 gallon of miscible oil was tested in 1935, and a 30:30:100 bordeaux mixture was tested in 1936 and 1937. The sprays were applied on the trunks of Grimes Golden trees after the dormant period when the apple buds were swelling.

One orchard, at Vincennes, Ind., was 12 years old in 1935. In this orchard the sprays were applied to pairs of tree rows alternating with pairs of unsprayed control rows. There was a total of 151 sprayed and 128 control trees. The other orchard, at Bloomfield, Ind., was 17 years old in 1935. The trees in two-thirds of the rows, comprising 235 trees, were sprayed, while every third row, comprising 135 trees, was left unsprayed as a control. During the years of the test, additional sprays for the control of apple scab and codling moth were applied to all the trees.

Cankers developed from natural infection on 3, 1, and 0.6 percent of the sprayed trees, and on 9, 4, and 0.8 percent of the unsprayed trees in the Vincennes orchard during the years 1935, 1936, and 1937, respectively. In the orchard at Bloomfield, cankers developed on

1, 0, and 0.4 percent of the sprayed trees and on 1, 0, and 1.5 percent of the unsprayed trees, during the years 1935, 1936, and 1937, respectively.

TREATMENT FOR CANKERS BY DECORTICATION

In August 1934, 13 cankers on 14-year-old Grimes Golden trees were treated by decortication. The diseased bark and the healthy bark for 4 cm. beyond the margins of the cankers and the infected and discolored wood beneath the cankers were removed (fig. 4, *E*). The wounds were then painted over with bordeaux-oil paint, as used by Zeller (*48*). The development of the cankers was permanently checked on 10 trees, while 3 showed slight development in restricted areas.

TREATMENT OF CANKERS WITH ZINC CHLORIDE AND SODIUM ARSENITE SOLUTIONS

The effectiveness of a number of chemical solutions in arresting the development of cankers was tested on Grimes Golden trees from 8 to 25 years old, at Bloomfield, Lafayette, Mitchell, and Vincennes, Ind. The solutions were applied with a brush to the surface of the cankers and to the bark in areas 5 cm. in advance of the cankers. The margins of the cankers when not readily evident were ascertained by probing with a knife, and marked by placing tacks at intervals. In a few treatments with zinc chloride, a thin layer of the outer bark at the advancing margins of cankers was removed with a knife before applying the solution.

Cankers treated with 10-percent copper arsenite in 10-percent ammonium hydroxide, 5- and 10-percent aqueous solutions of sodium arsenite, and Day's (*11*) solutions containing 43, 53, 64, or 71 percent of zinc chloride in acidified 74-percent alcohol, were not effectively controlled. The cutting away of the outer bark prior to treatment did not improve the effectiveness of the zinc chloride solutions.

Trunk cankers on 93 Grimes Golden trees were treated with a 10-percent solution of sodium arsenite in 50-percent alcohol during the fall of 1935. Only 1 of these cankers showed further enlargement when observed 5 weeks after treatment. Twenty-five untreated cankers continued to enlarge. The cankers were again observed after renewal of growth during the spring. None of the treated cankers showed renewed growth at that time. However, the data on possible renewed growth in the spring is inconclusive, since only 2 of the 25 untreated cankers renewed growth. The failure of the untreated cankers to enlarge in 1936 was an unusual occurrence, possibly associated with the effects of extremely low temperatures during January 1936. Of 13 cankers treated with the alcoholic sodium arsenite solution in 1936, 7 showed continued development 5 weeks after treatment. During 1937, 6 cankers were treated with this solution. Only 1 of these showed renewed activity in a restricted area when examined 6 weeks after treatment and again in 1938. Two untreated cankers continued to enlarge in 1937, and renewed enlargement in 1938. No deleterious effects of the solution on the upper portions of the trees were noticed during a period of 2 years after treatment. The solution was injurious to the bark, but the injury in all cases was confined to the treated area. The callus at the margins of treated cankers appeared to be retarded on a few trees.

DISCUSSION

Collar rot of uncertain origin on Grimes Golden and other varieties of apple has been reported by a number of investigators (*15*, *23*, *37*, *43*) during the years from 1900 to 1921. The symptoms described in many cases are similar to those of phytophthora collar rot. Furthermore, the varieties Grimes Golden and Thompkins King, often described by earlier workers as especially subject to collar rot, are shown to be most susceptible to phytophthora collar rot in the present work. The writer therefore believes that very likely many of these early reports deal with the phytophthora collar rot disease and that it has been an important cause of loss for many years.

The fact that the cankers in the incipient and actively enlarging stages are not easily detected by casual observation, may account for the failure of earlier workers to detect the causal relation of *Phytophthora cactorum* in the collar rot disease. Infected trees usually do not exhibit prominent symptoms until late in the fall and the second year after infection, at which time the cankers may not be very active. The causal fungus has not been obtained in culture from killed bark which had become dried and pulled away from the wood, and was isolated with difficulty from old cankers which were slightly active or had recently ceased enlarging.

In the physiologic specialization studies a limited number of inoculations were made with each of the 10 cultures tested on 30 varieties of apple trees other than Grimes Golden. Very likely more of the varieties would have been shown to be susceptible to one or more of the cultures had a larger number of inoculations been made. However the writer believes that the apparent differences in pathogenicity and selectivity of host variety exhibited by the cultures cannot be explained entirely on the basis of escape from infection. There is the possibility that the virulence of the cultures is altered with time on artificial media. This may have occurred in the case of culture No. 15, which was isolated from peony. The differences in pathogenicity of all the cultures on the varieties of apple trees, however, cannot be interpreted as traceable to a degeneration of pathogenicity of the cultures, since a number of cultures differing distinctly in pathogenicity were of recent isolation. Thus, cultures Nos. 1 and 8 were isolated in 1934, No. 13 in 1936, No. 14 in 1929, and No. 18 in 1932. Furthermore, cultures Nos. 12, 16, and 18 to 21, inclusive, which were nonpathogenic on 31 varieties of apple trees, were pathogenic on flax and peony plants. Müller (*28*) has shown that there are also physiologic races of *Phytophthora infestans* (Mont.) De Bary.

Grimes Golden trees, 2 to 4 years old, are resistant to infection even when inoculum is inserted in the bark. However, this resistance in the trunk is lost as the tree matures. Trees of resistant varieties are resistant at all ages. Bearing Grimes Golden trees with rough bark on their trunks are susceptible to infection by inoculum placed both on the surface of the trunk and in incisions in the bark. However, the large branches of bearing Grimes Golden trees are highly resistant to infection when the inoculum is inserted in the bark. The resistance of the large branches may be the same as that possessed by the young trees.

The component varieties of double- and high-graft Grimes Golden trees maintained their own specific reaction toward infection by

Phytophthora cactorum. This is in accord with the results obtained by Bond (*6*), Leach (*24*), May (*27*), Roach (*33*), and Salmon and Ware (*35*) in their respective investigations of the interaction of the stock and scion component parts of grafted plants on susceptibility and resistance to specific diseases. On the other hand, Hofmann (*21*), Richmond (*32*), and Wormald and Grubb (*47*) obtained evidence of an altered susceptibility or resistance of the stock and scion parts of grafted plants or their progenies to infection by specific organisms.

The most promising means of controlling the phytophthora collar rot disease of apple trees is the propagation of the susceptible varieties by grafting on desirable varieties of stocks that are resistant to the disease. The graft union of the susceptible variety with the resistant stock probably should be at least 30 inches or more above the soil line. From the standpoint of protection from phytophthora canker and from cold injury to the trunks and crotches of the trees, the more desirable practice would be to graft the susceptible varieties on the main branches of young trees of resistant varieties, after they have become established in the orchard.

Bordeaux mixture applied to the trunks of apple trees was only partly effective in preventing collar-rot infection. Fawcett (*13*, *14*) has recommended scarifying cankers and painting the resulting wounds with bordeaux paste for the control of phytophthora gummosis of citrus trees. He also advocated painting the trunks with bordeaux paste, and the application of a dust of zinc sulphate, copper sulphate, and hydrate lime (12 : 1 : 6) around the bases of young citrus trees, to prevent infection. Curzi (*10*) recommended decortication of infected tissues and applications of 3 to 5 percent bordeaux mixture as a treatment of phytophthora crown-rot cankers of peach.

SUMMARY

Phytophthora trunk canker, or collar rot, in 1933–34 caused serious losses in apple orchards in Indiana. In six orchards, from 21 to 68 percent of the Grimes Golden trees 14 to 18 years old were infected. In two of these orchards examined each year from 1935 to 1937, annual infection ranged from 0 to 6 percent. Evidence is presented in the review of literature which indicates that loss of Grimes Golden trees from phytophthora collar rot occurred in Indiana as early as 1900.

The disease is not easily detected in its early stages. The first outward symptom is a moist, discolored area on the surface of the bark. The infected bark is dark colored, has a strong fermented odor, and in later stages becomes dry, cracked, and drawn away from the wood. Frequently trees are girdled during one season.

Phytophthora cactorum is shown to be the casual agent of the Grimes Golden collar rot disease. The mycelium of the causal fungus develops both intercellularly and intracellularly, and penetrates all the tissues of the bark. Cultures of *P. cactorum*, pathogenic on apple trees, were isolated from active cankers, diseased fruits, and orchard soil. The fungus was also isolated from sapwood beneath a canker.

Evidence was secured of the existence of physiologic races of *Phytophthora cactorum*, which differ in their ability to infect varieties of apple trees. Certain cultures also differed in degree of virulence on the Grimes Golden variety. The Gano, Grimes Golden, Tompkins

King, Northwestern Greening, Rome Beauty, Smokehouse, and Stark varieties of apple trees were susceptible to one or more physiologic race of *P. cactorum* when artificially inoculated. Certain cultures of *P. cactorum* also were pathogenic on cherry, peach, and plum trees, and on flax and peony shoots. All 29 varieties of apple fruits tested were susceptible to fruit rot when artificially inoculated.

Grimes trees, 2 to 4 years old, were highly resistant both to artificial and to natural inoculation with *Phytophthora cactorum*. Older trees, 8 to 30 years old, were highly susceptible to infection from artificial inoculation. In the field the disease seldom occurs on trees less than 13 years of age. Differences also were found in the ease with which parts of the same tree were infected when inoculated. Trunks of bearing Grimes Golden trees were readily infected, while large branches were only occasionally infected when artificially inoculated.

The component varietal portions of double- and high-grafted Grimes Golden trees retained their specific resistance or susceptibility to *Phytophthora cactorum* unaltered by stock or scion influence.

The practice of grafting Grimes Golden scions on stocks at heights of 15 to 22 inches above the soil was found to be inadequate for the prevention of collar rot infection.

Bordeaux mixtures of the 16:16:100 and 30:30:100 formulae, were found to give partial control of collar rot infection. Day's solutions containing 43, 53, 64, or 71 percent zinc chloride were found to be ineffective in eradicating cankers on Grimes Golden apple trees. A 10-percent solution of sodium arsenite in 50-percent alcohol gave promise of being an effective means of checking the development of established cankers.

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GROWTH AND DISTRIBUTION OF ROOTS OF THE PERFECTION PIMIENTO IN GEORGIA[1]

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INTRODUCTION

The pimiento, or mild-flavored type of pepper (*Capsicum frutescens* L. var. *grossum* Bailey), is the most important vegetable cash crop grown in the lower piedmont section of Georgia, and from the standpoint of both value and quantity of pack, it ranks high among the commercial canning crops of the State. The acreage planted to pimientos in Georgia increased more than 35 percent from 1937 to 1938.

Growers often find difficulty in getting good stands of plants that will live and produce fruits until frost. Many of the plants are killed by the fungus *Sclerotium rolfsii*, but not all the losses can be attributed to this organism. Observations during the last four growing seasons have led the writer to conclude that another important contributing factor is the burning of the roots by the fertilizer applied. The method of fertilizer application may, therefore, be of considerable practical importance to the grower, but before this problem could be considered it was necessary to make a study of the development and distribution of the roots in the soil. The results of the study are reported in this paper.

MATERIALS AND METHODS

The study was conducted in the horticultural plots of the Georgia Experiment Station, which is situated in Spalding County, the center of the pimiento industry in Georgia. Although mechanical analysis shows the soil on which the plants were grown to be a sandy loam, it closely approaches the texture of a sandy clay loam, Cecil series, as interpreted by the classification of Davis and Bennett.[3] Both of these are predominant soil types of the pimiento-growing area.

A selected strain of Perfection pimiento seed was planted in an electrically heated hotbed on February 10, 1938. By February 20 most of the seeds had germinated and small plants were showing above the soil. In order to obtain a progressive knowledge of the development and distribution of the roots, an examination was made at the end of each 30-day period beginning February 28, 7 days after the seeds were up, and continuing through October 28, when the plants were approximately 8 months old. The first three examinations were made while the plants were growing in the hotbed. This was done by carefully removing the loose composted soil from around the roots with a hand fork and with water under light pressure from a garden hose.

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[2] The author is indebted to M. M. Murphy, Jr., of the Department of Horticulture, for taking the photographs used in this paper, and to L. C. Olson, of the Department of Agronomy, for assisting in taking the soil samples and for making the mechanical analyses.

[3] DAVIS, R. O. E., and BENNETT, H. H. GROUPING SOILS ON THE BASIS OF MECHANICAL ANALYSIS. U. S. Dept. Agr. Dept. Cir. 419, 15 pp., illus. 1927.

A few days prior to setting the plants in the field the soil was thoroughly prepared and fertilized with 600 pounds per acre of a 4–8–6 (N–P–K) fertilizer placed under the plants, as is the usual method of application for this crop. In order to facilitate handling and tracing the root system, two methods of spacing the rows and plants were used. The plants to be examined during the first 2 months after transplantation were set 5 feet apart in the row and the rows were spaced 5 feet apart. The rest of the plants were set 10 feet apart in rows spaced 10 feet apart, thus allowing ample room for root development in all directions. To avoid disturbing the roots during the growing season, weeds and grass were kept down by frequently scraping the plots with hoes rather than by cultivating them with plows.

The direct or digging method of examination, with the use of water under pressure in some cases to uncover the smaller roots, was employed in this work. (See fig. 8.) The method consisted of digging a trench by the side of the experimental plants to a depth below the deepest roots and of sufficient size to permit two persons to move about in it. The trench afforded a rather smooth perpendicular wall surface into which one could dig with a sharp hand pick and uncover and trace the root system. Several plants were examined in this manner each month. In some cases, especially on the older and larger plants, there were so many rootlets that it was impossible to show all of them in the drawings of the root systems. When this occurred a circular excavation (see fig. 13) was made around the plant, the inner face of which was 8 inches from the main stem of the plant, and the inner surface of the excavation was marked off into square feet with string. The root ends were then charted on coordinate paper in as nearly their exact position as it was possible to locate them.

Air temperature records were taken with a calibrated hygrothermograph at a point 12 inches above the soil among the plants, while the soil temperature was taken with a calibrated soil thermograph the bulb of which was placed among the roots 4 inches below the soil surface. Rainfall and evaporation records were secured from the nearby experiment station weather station.

Soil samples for mechanical and quick chemical analysis were taken from 20 holes dug at random over the field where the studies were being made. The holes, which were 36 inches wide, 54 inches long, and 36 inches deep, were large enough to permit accurate samples to be secured and further studies to be made of the various profile horizons in relation to root growth and distribution.

ROOT GROWTH IN THE HOTBED

Immediately after germination of the pimiento seed the young primary root typically grows directly downward. It penetrates the warm friable soil of the hotbed readily and by the time the plant is a week old it has usually reached a depth of 3 to 6 inches (fig 1, *A*). At this stage in the growth of the primary root no lateral or secondary roots can be detected. However, a few subsequent daily examinations show that they make their appearance within 8 to 10 days after germination, depending to a large extent on the moisture content and temperature of the soil. The first secondary roots originate at the upper extremities of the primary or taproot, and others develop

in rapid succession throughout its entire length with the exception of the immediate end.

At the time of the second monthly examination of the root system in the hotbed (March 28), it was found that most of the secondary roots were confined to about the first 3 or 4 inches below the soil surface (fig. 1, *B*). These roots extended outward in a somewhat horizontal direction to a distance of 6 inches on either side of the plant for a total spread of 1 foot, while the primary or taproot had increased in length to about 10 inches. Other lateral roots below this particular group had produced tertiary roots, all of which tended to penetrate the soil in a rather oblique or vertical direction.

By April 28, the last date on which the roots were examined in the hotbed, the lateral or secondary roots had increased in number, length, and size, as compared with those of the previous month (fig. 1, *C*). Some had reached a length of slightly over 10 inches, were very much branched, and averaged 0.6 mm. in diameter. The

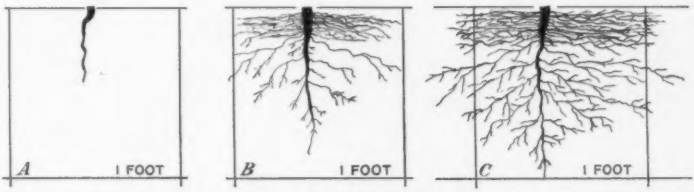

FIGURE 1.—Young primary root (*A*) of pimiento 7 days after germination and root system of the young pimiento plant 37 (*B*) and 68 (*C*) days after germination.

growth of the primary or taproot during this 30-day period, however. was only about one-half as much as that made by the laterals.

GROWTH AND DISTRIBUTION OF ROOTS IN THE FIELD

The heating units were turned off in the hotbed on March 31 and the plants allowed to harden. The total amount of rainfall in April exceeded by far the total amount of evaporation for the same period (table 1); thus the soil in the field remained in good physical condition and was well supplied with moisture during the entire month.

TABLE 1.—*Total monthly rainfall, evaporation, and rainfall-evaporation ratio during the 1938 growing season at Experiment, Ga.*

Month	Total rainfall	Total evaporation	R/E ratio	Month	Total rainfall	Total evaporation	R/E ratio
	Inches	*Inches*			*Inches*	*Inches*	
April	10.46	4.79	2.183	August	2.00	6.14	.325
May	3.14	7.05	.445	September	1.16	5.62	.206
June	8.48	7.39	1.147	October	.26	5.71	.045
July	5.88	6.34	.927				

The plants were carefully taken up from the bed and transplanted to the nearby field, as shown in the lay-out in figure 2, during the late afternoon of April 28. At this time they were about 68 days old, averaged 8 inches in height, and had many small flower buds. Wea-

ther conditions were ideal for the transplanting, and the plants scarcely wilted after being set out, but later it could be seen that the move had distinctly checked their growth.

The first examination of the root system in the field was made on May 27. Here, too, the effects of transplanting were evident in

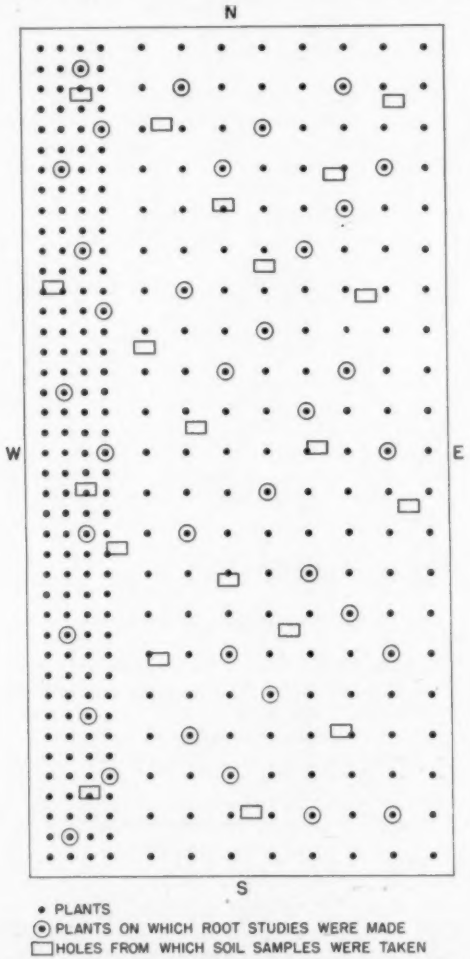

FIGURE 2.—Lay-out of plants in field after being transplanted from hotbed.

that the tap or primary root had been broken, which resulted in the initiation and development of a great many laterals (fig. 3). Although the spread of the root system was practically the same as that of the previous month, about 24 of the older and more prominent lateral roots had increased to 1 mm. in diameter. From these, as well as from the stub of the old taproot, grew the new secondary and tertiary

roots. These findings concerning the effects of transplanting young pepper plants on lateral root formation are in complete agreement with those of Weaver and Bruner,[4] who studied the development of the root system of the Bell, or Bull Nose, variety of pepper under

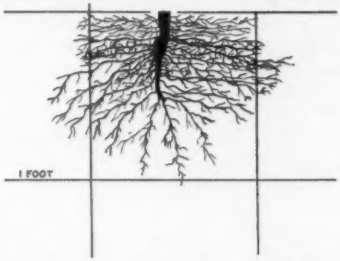

FIGURE 3.—Root system of pimiento 30 days after being transplanted to the field.

field conditions at Norman, Okla. On May 27, the vertical penetrating roots were found to extend 14 inches deep. These roots, together with their young laterals and the ones from the old taproot immediately above, almost completely filled the surface foot of soil at the end of the first 30-day period in the field.

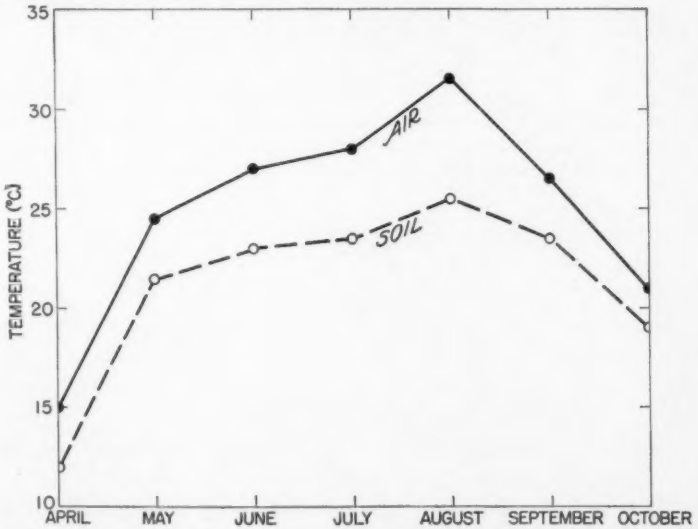

FIGURE 4.—Air and soil temperatures in the pimiento field during the experiment.

With approximately 8½ inches of rainfall during June and an average atmospheric and soil temperature of 27° and 23° C. respectively (table 1 and fig. 4) conditions for plant growth were relatively good.

[4] WEAVER, JOHN E., and BRUNER, WILLIAM E. ROOT DEVELOPMENT OF VEGETABLE CROPS. 351 pp., illus. New York. See pp. 268–273.

A second field examination was made on June 27. The plants at this stage averaged 16 inches in height and had a spread of 22 inches. There were many buds and blooms and also a few green fruits, the largest of which scarcely exceeded 7 mm. in diameter

The stem was 13 mm. in diameter at the surface of the soil and tapered gradually to a rather blunt root end which extended 6 inches in depth, the taproot having been broken in transplanting. As will be recalled, in the above examinations the prominent part of the root

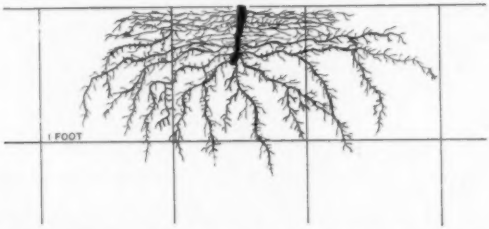

FIGURE 5.—Root system of the pimiento 60 days after being transplanted to the field.

system consisted of many laterals. Some of these had now extended outward 18 inches, mostly in the A horizon or surface 6 inches of soil, and measured 1.5 mm. in diameter. Other shorter ones ran for distances of 4 to 12 inches. They had branched at the rate of 4 to 10 laterals per inch and ranged from ½ to 1½ inches in length. Nearly all the larger roots extended horizontally or slightly obliquely downward for some 10 to 14 inches and then turned downward and ran vertically or again obliquely to a maximum depth of 16 inches (fig. 5).

By the date of the third field examination, July 28, the plants had

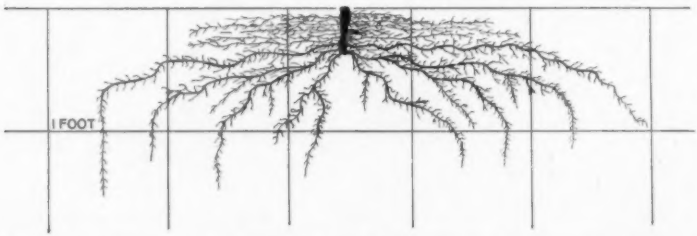

FIGURE 6.—Root system of the pimiento 90 days after being transplanted to the field.

attained an average height of 26 inches and a spread of 25 inches. The old stubby portion of the taproot measured only a little more than 5 inches in length but had a large number of lateral roots growing out from it in all directions, some as long as 30 inches. The majority of these roots, however, were confined to a radius of 24 inches. The larger ones were attached near the end of the old primary or taproot (fig. 6) and measured 3 mm. in diameter, while the smaller secondary roots, although relatively short and averaging but 1 mm. in thickness, were numerous and very well branched. Some of them were found

within the first inch of topsoil. As during the previous examination it was found that the longer roots, after running in a horizontal direction for 18 to 20 inches, turned downward in an oblique and some in a distinctly vertical direction. The vertical penetrating roots had at this stage reached a maximum depth of 20 inches. One small root, however, was traced to a depth of 26 inches but was not included in the drawing because a closer examination revealed that it had not penetrated the subsoil normally but had followed the course of a channel made by the root of a pecan tree that in former years had grown close by.

As shown in table 1, only 2 inches of rain fell during August, while the total evaporation for the month was 6.14 inches, giving a rainfall-evaporation ratio of 0.325. The accompanying average air temperature was 31.5° C., the highest recorded for the entire growing season. During this 30-day period the plants grew less than 2 inches in height, although it will be seen below that root extention proceeded at a rapid rate.

The fourth field examination of roots was made on August 27. The taproot at this stage of growth was 45 mm. thick at the soil

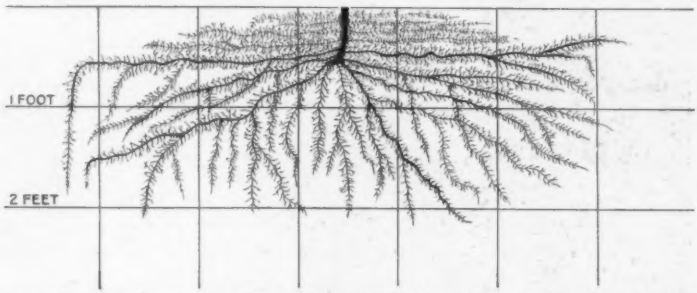

FIGURE 7.—Root system of the pimiento 120 days after being transplanted to the field.

surface, tapered to a diameter of 13 mm. at the end, and gave rise to many laterals. The previously small roots found in the surface 6 inches of soil had increased greatly in both diameter and length. Many were as much as 1.5 mm. in thickness and extended horizontally for a distance of 24 inches. The larger roots near the base of the taproot had made even greater growth (fig. 7). From 6 to 10 were found that measured as much as 6 mm. in diameter. Even as far as 2 feet from the base of the plant some of these strong roots were 2.5 to 3 mm. thick. The maximum lateral spread of the root system had increased from 29 inches in July to 40 inches in August for a total gain in root length of 11 inches. It will be noted further in figure 7 that nearly all the larger and more deeply penetrating roots again ran horizontally for about 24 inches and then turned obliquely downward near their extremities or else abruptly downward and paralleled the course of the old taproot. However, the vertical growth at this stage, reaching a little more than 2 feet in depth, had not kept pace with that horizontally, due in all probability to the difference in soil texture and compactness. Some properties of the A and B horizons of the Cecil sandy loam soil are shown in table 2.

From the large vertically growing roots mentioned above numerous smaller roots originated, and most of these grew in the same vertical direction. These roots ranged in length from 6 to 18 inches and

FIGURE 8.—Lateral root growth in the A soil horizon of the pimiento 150 days after being transplanted to the field.

averaged approximately 0.6 mm. in diameter. Some had rebranched and all were covered with young rootlets at the rate of three to eight per inch. This network of roots was, no doubt, very effective in bsorbing moisture.

TABLE 2.—*Some properties of a typical Cecil sandy loam soil profile in the pimiento-growing district of central Georgia, 1938*

Profile layer	Depth of layer	Description of layer	Combined sand	Clay	Silt	pH
	Inches		*Percent*	*Percent*	*Percent*	
A	0–6	Brownish-red sandy loam	69.9	17.2	12.9	4.89
B	6–50	Red, stiff clay	45.6	45.7	8.7	4.76

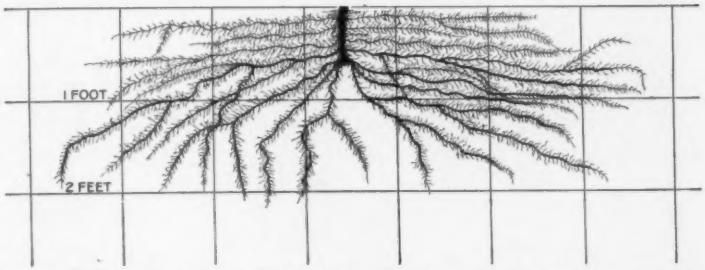

FIGURE 9.—Root system of the pimiento 150 days after being transplanted to the field.

By the time the September examination was made the plants had been growing in the field for 5 months. Owing to a prolongation of the

FIGURE 10.—Extent of lateral root growth of a mature pimiento plant.

drought and hot weather, the top growth was very little greater than that of the previous month, but root growth was still making progress. The smaller and more fibrous lateral roots of the A horizon

now extended outward as far as 32 inches from the base of the plant and were so numerous that they completely filled that portion of the soil (fig. 8). Many of them were relatively close to the soil surface. The larger, horizontally growing roots from near the base of the

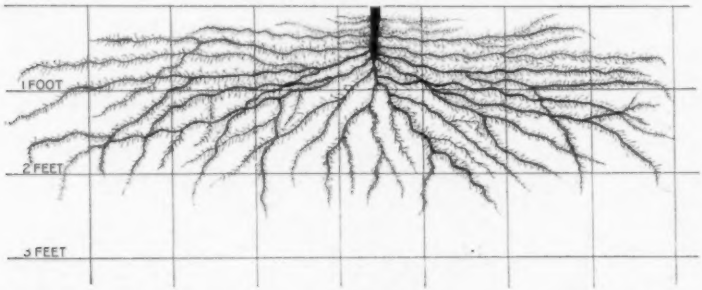

FIGURE 11.—Part of the root system of the pimiento 180 days after being transplanted to the field.

old taproot made about 6 inches if growth in September. They now extended outward 36 inches on all sides of the plant, having a total spread of 6 feet, and some measured as much as 10 mm. in diameter at the largest point. As can be seen in figure 9, however,

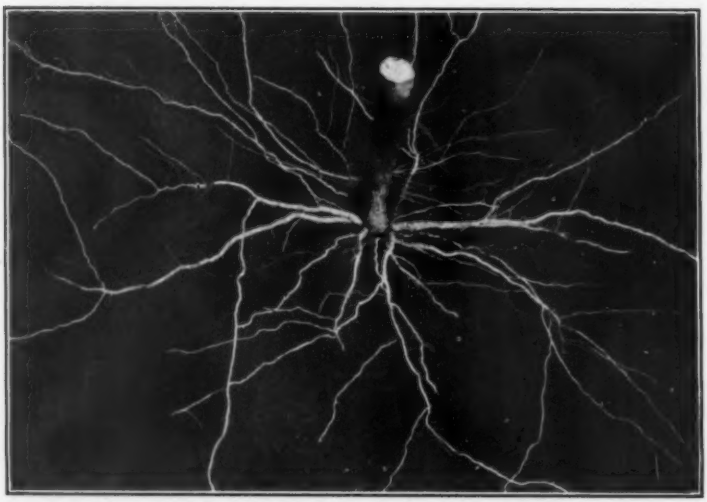

FIGURE 12.—Upper part of the primary root of a mature pimiento plant showing absence of laterals.

the progress made by the roots in penetrating the heavy clay-subsoil was small as compared with that of similar roots examined a month earlier.

As the average date of the first killing frost in central Georgia is November 10, the final monthly examination of roots was made on

October 28. The plants averaged 34 inches in height and 29 inches across. They were loaded with fruits of all ages and some were still blooming. As is shown to some extent in figure 10, and more in

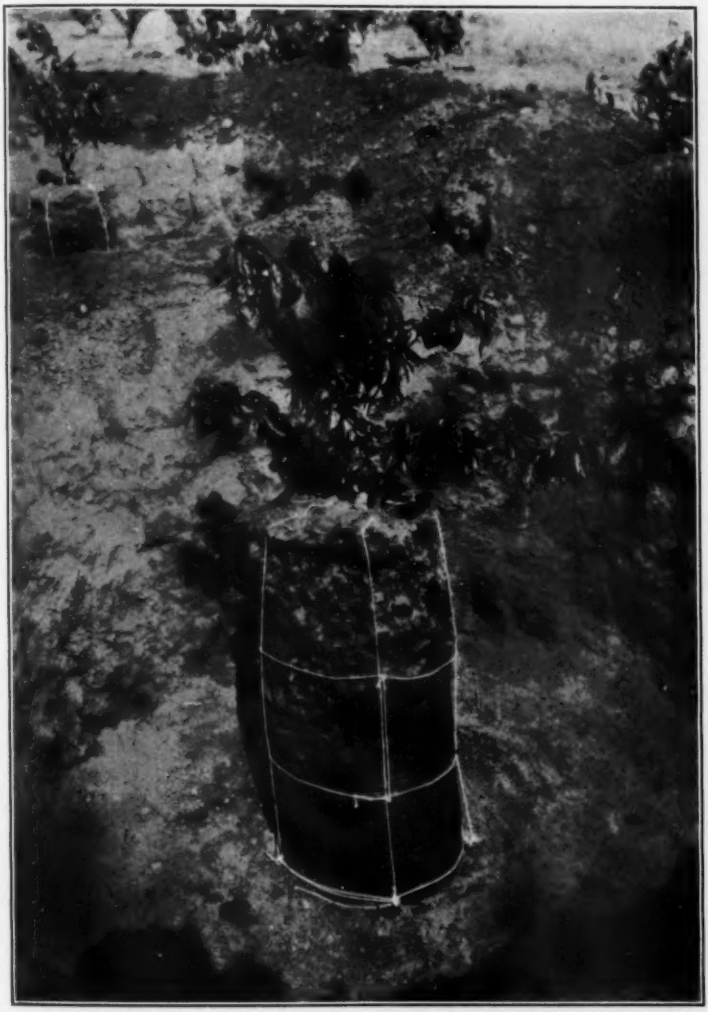

FIGURE 13.—Mature pimiento plant removed by the circular method of excavation.

detail in figure 11, the root system now extended outward to a distance of 48 to 52 inches from the base of the plant. As a rule the horizontally growing roots were a few inches longer when growing parallel with or in the immediate row channel than when at right angles

to it. The larger and more prominent of these roots usually turned downward about 30 inches from the place of attachment and extended well into the second foot of soil. The distinctly vertically penetrating roots generally extended a few inches deeper. Thirty-two inches was the maximum depth at which any roots were found during the experiment and only a few of these appeared in the October excavation.

It is to be noted particularly in figures 11 and 12 that lateral roots are not always initiated throughout the entire length of the primary or upper portion of the taproot, especially in plants that are grown on heavy clay-loam soils. Neither deep setting nor high mounding of the plants under field conditions was found to have any noticeable

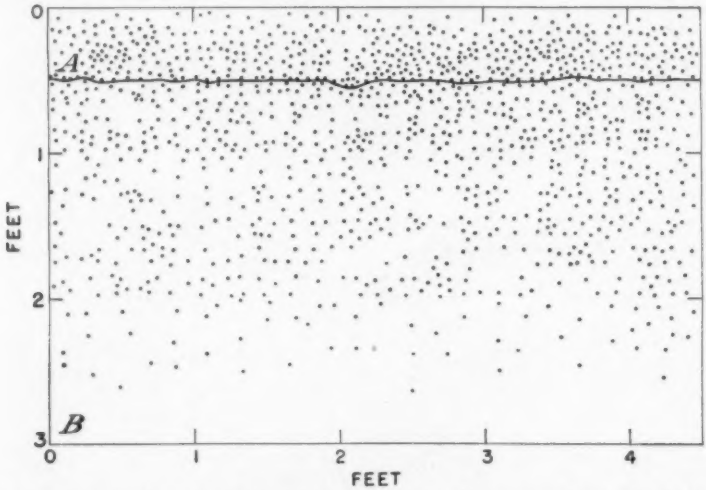

FIGURE 14.—Root concentration and penetration of a mature pimiento plant in two soil profile horizons. Each dot represents a root end.

effect on lateral root initiation at points above those at which they ordinarily occur.

The second method employed for studying the distribution of roots of mature plants (figs. 13 and 14), which is similar to that used on deciduous fruit trees by Oskamp,[5] also showed that the pimiento roots thoroughly occupy the soil from within a few inches of the surface to a depth of 24 inches. Some roots extend deeper, as was found by the first method of study, but with an increase in depth below 24 inches there is a corresponding decrease in both number and size of roots.

In general conformation the root system of the Perfection pimiento as found in this study is much the same as that reported by Weaver and Bruner [6] for the Bell, or Bull Nose, variety of pepper. The results of this study also substantiate in large measure those obtained by Mohammad and Deshpande [7] in similar work on chilies in India.

[5] OSKAMP, JOSEPH. THE ROOTING HABIT OF DECIDUOUS FRUITS ON DIFFERENT SOILS. Amer. Soc. Hort. Sci. Proc. (1932) 29: 23-219, illus. 1933.

[6] See footnote 4.

[7] MOHAMMAD, ALI, and DESHPANDE, R. B. STUDIES IN INDIAN CHILIES. 2 THE ROOT SYSTEM. Agr. Jour. India 24: 251-258, illus. 1929.

DISCUSSION

At present the usual spacing of pimiento plants in central Georgia is 18 to 36 inches in rows 36 to 42 inches apart. Within the first 3 months after the plants are transplanted to the field their roots thoroughly occupy the soil both in and between the rows and many of them are relatively close to the surface. Largely as a matter of custom pimiento growers cultivate their plants regularly about every 2 weeks whether there are weeds to be killed or not. There is little justification for this practice, for it cuts nearly all of the shallow feed roots between the rows and makes it impossible for the plants to utilize the maximum amount of nutrients in the soil. The effects of this practice are especially detrimental in late dry seasons when the plants are loaded with mature fruits. Weed-control measures should be instituted if possible before the weeds can become established and compete with the crop for moisture and nutrients. When no weeds are present and a soil mulch has formed, cultivation is an unnecessary expense.

As much as 100 to 200 pounds per acre of extra commercial fertilizer is usually applied as a side dressing around pimiento plants twice during the growing season, the first about June 1 and the second in early September. In the light of the results of this investigation, it appears that a greater utilization of the fertilizer may be accomplished if it is scattered over the entire area between the rows, rather than in bands near the base of the plants.

SUMMARY

As soon as the pimiento seed germinates in the hotbed, which usually takes about 10 days, the young primary root grows typically directly downward. After 2 months in the hotbed, with relatively good care, the plants are well hardened and ready to be transplanted to the field. At this stage the primary root extends down to about the 10- to 12-inch level and is well supplied with laterals measuring from 4 to 10 inches in length and about 0.6 mm. in diameter.

The primary or taproot is usually more or less damaged in the process of transplanting. The remaining short portion of the taproot does not appear to make up a very important part of the root system as such, but from this and the base of the stem arise many laterals, except in some cases on heavy clay soils, that continue to develop and eventually constitute a very efficient absorbing system. These roots grow horizontally outward to vertically downward and by the time they have been in the field for 60 days they completely occupy the soil on all sides of the plant to a depth of 10 to 14 inches. By the last of August the larger and more deeply penetrating roots extend outward 40 inches from the base of the plant and downward as deep as 26 inches. Mature or 8-month-old plants have a root spread of 48 to 52 inches on each side, many of the laterals being found in the second foot of the soil. Relatively few roots penetrate the stiff clay subsoil deeper than 24 inches.

A STATISTICAL STUDY OF WINTER PAUSE IN WHITE LEGHORN PULLETS [1]

By I. MICHAEL LERNER, *junior poultry husbandman*, and LEWIS W. TAYLOR, *head*, *Division of Poultry Husbandry, California Agricultural Experiment Station* [2]

INTRODUCTION

The character commonly referred to as winter pause has been recognized for a long time. However, its nature or the factors bringing about its expression are still largely unknown. Goodale (*1*, *2*) [3] considered that both hereditary and environmental factors were responsible. In a later report, Goodale and Sanborn (*3*) found that duration of pause could apparently be reduced by selection. On the other hand, indication of seasonal incidence was seen in the fact that 90 percent of the birds in their flock that started to lay in September exhibited winter pause, while of those that started to lay in December only 30 percent paused. Hays seems to be the only other worker who has pursued extensive studies on the subject. As early as 1924 he (*4*) suggested a single recessive factor for 7-day or longer pauses. In 1926 Hays and Sanborn (*7*) presented correlations between the length of winter pauses of 4 days or more and hatching date (−0.2480), date of first egg (−0.3205), age at first egg (−0.2329), and length of the laying period before the pause (−0.1385, the correlation ratio being 0.2199).

In 1936 Hays (*6*) presented similar correlations as well as correlations between winter-pause duration and a whole series of other production factors. Most of these, however, illustrate relations with post-pause characters. North (*8*) found that pausing caused an increase in body weight and two or more pauses an increase in egg weight.

The present study attempts to analyze statistically the nature of winter pause and its expression.

MATERIAL AND METHODS

In a study of such an ill-defined character as winter pause, a series of arbitrary definitions must be set up. Although any conclusions reached will of necessity apply only to the populations considered and to the factors defined at the outset, a better understanding may ensue from studies of this type. The writers believe that, while studies on experimental physiology will ultimately explain the mechanism of operation of the factors determining annual production, further preliminary biometric studies to point the way to experimental verification are needed.

Accordingly, two populations of Single-Comb White Leghorn pullets were selected from the station flock. The J population included 768 pullets hatched in 5 groups at intervals of 1 week, beginning March 20, 1934. The K population consisted of 626 pullets hatched in 4 groups

[1] Received for publication January 9, 1939.
[2] Assistance in calculation of statistical constants was provided by the Works Progress Administration, official project A. P. No. 465-03-3-209.
[3] Italic numbers in parentheses refer to Literature Cited, p. 210.

at weekly intervals, beginning March 19, 1935. The basis of selection of both groups from pullet flocks numbering about 1,200 in the J series and 1,100 in the K series consisted of the following criteria, only birds answering these requirements being included:

Birds maturing before January 1.
Birds alive on July 1 of their second year of life.
Birds which did not exhibit broodiness before March 1.
Birds which were not floor layers at any time.
Birds which, if they paused before March 1, resumed laying before July 1.
Birds which had at least 19 sisters or half-sisters by a common sire, answering all of the above requirements.

Twenty sire families constituted the J series and 17 sire families the K population.

Winter pause is defined as a continuous nonlaying period of 7 days or longer beginning after at least one egg was laid, and before March 1. The factors studied were: (1) Percentage of the birds in a sire family, in a hatch, or in a series, which exhibited one or more winter pauses; (2) average duration of the pauses; (3) frequency of occurrance of pauses per pausing bird; (4) degree of pausing, which represents the loss in productive days due to pause in any given period; and (5) date and age on the first day of pause.

The degree of pausing, calculated as the percentage of pausing hen-days in any given period, is considered as an index expressing the extent of pausing in any of the groups considered. The degree of pausing was calculated for twelve 10-day periods from November 1 to February 28, inclusive. It is important to note that this includes all pauses as here defined irrespective of the causative factors involved, of which many may be in operation.

Prepause factors considered in this study include the date of hatch, the date of first egg, and the age at first egg of all the pullets in a sire family and of the pullets which later exhibited winter pause.

The total degree of pausing in the two populations differed markedly, the K series showing only somewhat over half the pausing observed in the J series. The data for the latter will be presented first, and only such K series data as do not show agreement with the observations on the J population will be given.

DATA ON THE J SERIES

Data on the J series were analyzed from two standpoints: (1) As one population, irrespective of descent, and (2) as 20 separate sire families in order to determine the genetic implications of the relation between the different factors studied.

Table 1 presents the pausing characteristics of this population with respect to date of hatch. The degree of pausing is highest in the earliest hatches and decreases regularly in the later hatches. The same trend may be noted with respect to the percentage of pausing birds. However, the frequency of pausing and the average duration of pause seem to have no relation to the date of hatch. From the average age at pause onset, which tends to decrease with the date of hatch, it may be seen that in this population the factor bringing on pause operated approximately at the same time. This is borne out by the average date of pause onset, which fell within a period of 14 days in the five hatches studied. Apparently seasonal and age effects are both responsible for the condition of winter pause. Once the birds

pause, however, their age has no effect on the length of time they stay out of production.

Table 2 presents an analysis of variance of degree of pausing between and within the 10-day periods between November 1 and February 28. This analysis, made by pooling the variances for the sire families, indicates significant differences between periods in degree of pausing. Furthermore, the table also shows that there are differences between the families of the different sires and gives the variance between hatches and periods, thus indicating three significant factors in the degree of pausing: (1) Season (between periods), (2) age (between hatches), and (3) inheritance (between sire families). A triple criterion analysis (hatch, period, sire) was not attempted because the numbers in the subclasses are disproportionate, and some of the subclass numbers would be so small as to render the determination of degree of pausing inaccurate.

TABLE 1.—*Characteristics of the J series with respect to date of hatch*

Date of hatch	Total birds	Proportion of birds pausing	Total pauses	Pauses per pausing bird (frequency)	Average age at pause onset	Average date at pause onset	Average duration of pause	Degree of pausing
	Number	*Percent*	*Number*		*Days*		*Days*	
Mar. 20	237	84.0	323	1.62	257	Dec. 2	28.2	28.6
Mar. 27	130	71.5	125	1.34	253	Dec. 5	31.1	23.4
Apr. 3	124	62.1	123	1.60	257	Dec. 16	25.1	19.0
Apr. 10	193	64.2	180	1.45	240	Dec. 6	24.9	18.9
Apr. 17	84	48.8	58	1.41	239	Dec. 12	25.3	13.2
All hatches	768	69.5	809	1.51	252	Dec. 6	27.2	21.9

TABLE 2.—*Analysis of variance of degree of pausing, J series, between and within 10-day periods from November 1 to February 28*

Source of variance	Degrees of freedom	Sum of squares	Mean square
Total	2,399	496,339	
Between periods	11	460,771	41,888
Within periods	2,388	35,568	15
Total	239	56,546	
Between sire families	19	10,593	558
Between periods	11	35,156	3,196
Remainder	209	10,797	52
Total	59	9,671	
Between hatches	4	1,655	414
Between periods	11	6,283	571
Remainder	44	1,733	39

The trend of degree of pausing by the 10-day periods can be seen from table 3, which gives the distribution by sires and periods. The family showing the highest degree of pausing is that of sire G36 with a degree index of 37.7; the lowest degree observed is 11.8 for sire F15, the other sire families falling within this range. The significant point in this table is that 14 out of the 20 sire families show the mode of pausing in the same period (December 1–10); 4 families have a mode in the neighboring periods. Only 2 of the families show modes in other periods and only 1 of these differs significantly

from the degree of pausing in the December 1–10 period. The significance of differences between any 2 cells may be ascertained from the values given in the footnote to the table. Table 3 thus presents further evidence for the interpretation of table 2 so far as sire family and period differences are concerned.

Table 4 supplies similar evidence with respect to the effect of hatch. The mode for the whole of the population falls in the period of December 1–10, three earlier hatches showing the highest degree of pausing during that period. The two later hatches have modes in the preceding period which, however, are not significantly higher than the degree-of-pausing values for these hatches for the modal period of the whole population.

Degree of pausing was broken down into its constituents: (1) Percent of birds exhibiting pause, (2) frequency or number of pauses per pausing bird, and (3) average duration of each pause. These, together with date of pause onset, were analyzed with respect to differences between hatches and to differences due to variation in the date of first egg. To facilitate the analysis of variance, the periods of maturity here selected (September 18 to November 17) were such as to have representatives of all hatches in each of the four 15-day periods. This included 718 of the 768 birds in the J series.

TABLE 3.—*Distribution of degree of pausing by sires and by periods, J series* [1]

Period	Degree of pausing classified by sire and number of daughters as indicated									
	F15, 29	H58, 35	H62, 48	G14, 65	H42, 29	H79, 78	H8, 42	H90, 66	H91, 39	H39, 24
Nov. 1–10	20.0	13.9	5.3	5.2	4.8	13.8	2.1	6.0	12.3	0
Nov. 11–20	15.4	14.9	13.7	15.9	4.0	15.7	13.5	11.1	22.0	15.3
Nov. 21–30	*51.8*	27.9	27.4	35.5	13.7	29.6	35.9	17.9	39.4	42.9
Dec. 1–10	29.2	*55.4*	*51.2*	*41.5*	28.2	*53.2*	*42.7*	30.5	*51.5*	*50.3*
Dec. 11–20	14.7	22.4	19.9	31.2	28.2	28.0	32.4	*50.7*	39.0	36.0
Dec. 21–30	5.0	17.8	14.1	21.3	28.8	25.5	28.1	23.4	24.0	38.1
Dec. 31–Jan. 9	12.2	8.7	16.0	19.2	*37.9*	24.0	27.4	26.3	24.0	31.9
Jan. 10–19	8.2	4.2	14.8	13.8	32.1	20.6	22.3	24.5	15.6	36.7
Jan. 20–29	2.4	.3	7.2	6.0	21.9	17.0	16.0	21.8	8.9	16.5
Jan. 30–Feb. 8	2.1	.9	5.8	1.5	10.5	11.8	10.0	17.9	3.6	2.8
Feb. 9–18	0	2.1	5.8	4.5	8.5	9.2	5.7	17.6	5.6	0
Feb. 19–28	0	1.2	4.8	3.1	8.7	4.7	5.0	19.7	3.8	0
Total degree of pausing	11.8	12.3	13.8	16.6	18.9	19.4	20.1	20.6	20.8	21.2

Period	Degree of pausing classified by sire and number of daughters as indicated									
	G52, 50	G5, 27	H60, 29	H64, 30	H43, 34	H46, 31	H37, 20	H25, 23	H33, 38	G36, 31
Nov. 1–10	14.4	4.5	15.8	15.6	9.0	2.1	4.5	19.6	27.2	15.5
Nov. 11–20	27.0	26.0	24.1	15.8	10.8	13.0	10.0	20.3	23.7	25.0
Nov. 21–30	41.6	46.9	*55.6*	39.5	32.7	33.8	33.8	55.5	41.5	41.5
Dec. 1–10	*45.0*	*58.8*	41.0	*48.3*	*58.5*	*55.0*	*51.0*	*64.2*	48.2	55.8
Dec. 11–20	39.8	40.8	33.1	43.1	43.3	45.2	47.5	47.8	*50.0*	58.9
Dec. 21–30	32.2	30.0	31.2	34.9	32.0	43.2	28.5	50.0	41.3	55.9
Dec. 31–Jan. 9	26.0	27.2	27.3	32.8	41.6	44.7	45.0	43.0	43.7	*60.9*
Jan. 10–19	16.4	18.2	17.9	30.8	31.7	30.9	44.5	33.5	39.4	55.8
Jan. 20–29	13.2	14.6	9.8	23.0	26.3	21.8	34.0	22.5	31.9	40.1
Jan. 30–Feb. 8	9.0	10.1	14.7	20.3	21.5	13.0	20.0	9.3	22.5	22.7
Feb. 9–18	4.6	.8	8.9	10.0	9.6	22.4	15.5	15.4	19.2	11.8
Feb. 19–28	3.8	0	2.8	5.5	5.1	14.0	11.0	4.1	9.8	8.0
Total degree of pausing	22.8	23.2	23.5	26.6	26.8	28.3	28.8	31.4	33.2	37.7

[1] 6.7 constitutes a significant, and 9.2 a highly significant difference between any 2 cells.

Modes in italic figures.

TABLE 4.—*Distribution of degree of pausing with respect to date of hatch in the J series* [1]

Period	Data for date of hatch indicated					
	Mar. 20	Mar. 27	Apr. 3	Apr. 10	Apr. 17	All hatches
Nov. 1–10	12.2	7.3	8.0	10.1	13.8	10.3
Nov. 11–20	16.3	10.9	14.8	20.8	20.6	16.6
Nov. 21–30	45.3	33.6	21.9	*35.2*	*24.4*	34.4
Dec. 1–10	*59.2*	*47.6*	*30.6*	32.4	20.9	*41.9*
Dec. 11–20	50.3	43.4	25.6	23.3	17.7	34.9
Dec. 21–30	42.5	33.2	20.1	18.2	18.4	28.4
Dec. 31–Jan. 9	36.5	31.0	27.8	24.4	12.8	28.5
Jan. 10–19	27.1	30.5	22.8	19.1	12.7	23.4
Jan. 20–29	19.9	19.9	16.7	11.6	10.7	16.8
Jan. 30–Feb. 8	15.7	10.1	14.3	8.0	2.9	11.5
Feb. 9–18	11.2	8.7	14.5	6.0	1.3	9.3
Feb. 19–28	7.0	5.1	11.0	5.1	1.7	6.6
Total degree of pausing	28.6	23.4	19.0	17.9	13.2	21.9

[1] Modes in italic figures.

Table 5 presents this analysis and indicates that date of first egg has more influence on the date of pause onset and on duration of pause than has date of hatch, while the latter has a greater influence in determining the percentage of birds in a population exhibiting pause. Frequency of pause or occurrence of repetitional pausing by the same bird seems to be independent of either date of hatch or date of first egg.

TABLE 5.—*Analysis of variance of pausing characters in the J series*

Source of variance	Degrees of freedom	Date of pause onset		Percentage of birds pausing		Frequency of pause		Duration of pause	
		Sum of square	Mean square	Sum of square	Mean square	Sum of square	Mean square	Sum of square	Mean square
Total	24	3,373	.....	72,106	.....	16.15	.....	1,303	.....
Between hatches	4	315	78.8	28,564	[1] 7,141	3.46	0.865	260	65.0
Between dates of first egg	4	1,874	[2] 468.5	7,271	1,818	2.28	.570	708	[2] 177.0
Remainder	16	1,184	74.0	36,721	2,267	10.41	.651	335	20.9

[1] Significant. [2] Highly significant.

Although the date of first egg apparently bears no relation to the proportion of birds in the population which pause, this does not hold true within sire families. Thus, the date of first egg of pausing half-sisters is 9.85 days earlier than that of the nonpausing birds in the same family. The t value for 19 degrees of freedom is 6.5405, which indicates that this difference is highly significant.

The genetic implications involving the factors discussed were analyzed by means of correlations between the characteristics exhibited by sire families. With 20 sires represented in this population, 18 degrees of freedom for the zero-order correlations were available. Table 6 gives the coefficients of correlation and indicates that:

1. Frequency of pauses is not correlated with any of the other factors studied.

2. Date of pause onset is not correlated with any of the other factors studied.

3. Date of first egg of pausing birds is correlated with the percentage of birds in the sire family which exhibit pause, the correlation coefficient being 0.5127.

4. Percentage of pausing birds in the sire family is not correlated with average duration of pause.

5. The degree of pausing shows the greatest correlation with the percentage of pausing birds (0.7421), followed by the correlation with duration of pause (0.5869).

TABLE 6.—*Zero-order correlation coefficients between characteristics of sire families in the J series* [1]

Character studied	B	C	D	E	F	G
A. Date of first egg of all birds	0.9309	0.3762	0.1355	−0.2852	0.3043	0.0947
B. Date of first egg of pausing birds		.3825	.0302	−.2233	.5127	.2356
C. Date of pause onset			−.2815	.4200	.1935	.2950
D. Frequency of pause				−.3226	−.1733	−.0265
E. Duration of pause					.1476	.5869
F. Percentage of birds pausing						.7421
G. Degree of pausing						

[1] r at $P=0.05$ is 0.444; r at $P=0.01$ is 0.561.

The coefficient of multiple correlation, with degree of pausing as the dependent variable and frequency of pause, duration of pause, and percentage of pausing birds as the independent variables, was found to be 0.9225, giving 85 percent determination. Complete determination of degree of pausing by these three independents is not attained, since the measurement of degree is confined to the period between November 1 and February 28, while some of the pauses started before, and others continued beyond these dates.

TABLE 7.—*Characteristics of the K series with respect to date of hatch*

Date of hatch	Total birds	Proportion of birds pausing	Total pauses	Pauses per pausing bird (frequency)	Average age at pause onset	Average date at pause onset	Average duration of pause	Degree of pausing
	Number	*Percent*	*Number*		*Days*		*Days*	
Mar. 19	127	55.1	109	1.56	246	Nov. 20	26.2	11.8
Mar. 26	166	48.8	141	1.74	246	Nov. 27	28.6	13.2
Apr. 2	179	46.4	127	1.53	249	Dec. 7	26.4	12.3
Apr. 9	154	34.4	74	1.40	249	Dec. 14	24.5	8.3
All hatches	626	45.8	451	1.57	248	Dec. 2	26.7	11.4

DATA ON THE K SERIES

The characteristics of the K series of birds are presented in table 7. A comparison of this table with table 1 shows considerable differences in the pausing characters of the two populations. Thus, the degree of pausing in the J series is nearly twice that exhibited by the K pullets. The trend in the latter with respect to date of hatch is not so uniform as that found in the J birds, although the last hatch shows the least amount of pause. The percentage of pausing birds is considerably higher in the J series, while pause frequency and pause duration are not markedly different in the two populations. The most significant

differences between the J and the K series lie in the average age and the average date of pause onset in the different hatches, although when each population is considered irrespective of hatching dates, these differences are not marked. While the pauses in the different hatches of the J series occurred at approximately the same date, the K population showed increasingly later onset of pause with the later date of hatch. As a consequence, in the J series the pausing birds in the late hatches were younger than those in the early hatches at the time of pause onset, whereas in the K series a uniformity in age of pausing birds, irrespective of date of hatch, obtained.

TABLE 8.—*Distribution of degree of pausing with respect to date of hatch in the K series* [1]

Period	Data for date of hatch indicated				
	Mar. 19	Mar. 26	Apr. 2	Apr. 9	All hatches
Nov. 1–10	10.6	14.3	9.1	4.9	10.0
Nov. 11–20	12.9	11.5	13.7	9.6	11.6
Nov. 21–30	13.1	13.2	16.7	10.6	13.4
Dec. 1–10	10.0	*16.3*	*20.9*	*13.4*	*15.4*
Dec. 11–20	13.4	15.6	19.4	11.5	15.3
Dec. 21–30	12.6	9.7	11.7	8.8	10.5
Dec. 31–Jan. 9	12.2	12.0	7.7	3.3	8.7
Jan. 10–19	*15.8*	14.1	10.5	7.0	11.7
Jan. 20–29	14.6	15.8	11.8	8.6	12.7
Jan. 30–Feb. 8	9.0	11.9	10.1	11.2	10.8
Feb. 9–18	7.7	12.4	9.3	6.4	9.0
Feb. 19–28	9.2	11.7	6.7	4.8	8.6
Total degree of pausing	11.8	13.2	12.3	8.3	11.4

[1] Major modes in italic figures.

A further difference in the behavior of the 2 series may be observed from the comparison of tables 4 and 8, which give the distribution of the degree of pausing in the respective series by periods. Whereas the J series in general gives a unimodal type of distribution, the K series invariably shows 2 or more peaks for each hatch. The reasons for these observed differences are somewhat obscure. It is not certain that the reduction in number of pauses (809 pauses in a flock of 768 birds or 1.05 per bird in the J series; 451 pauses in a flock of 626 birds or 0.72 per bird in the K series) did not lead to the differential behavior observed.

TABLE 9.—*Zero-order correlation coefficients between pause characters of sire families in the K series* [1]

Character studied	B	C	D	E	F	G
A. Date of first egg of all birds	0.8334	0.2920	−0.0997	−0.2726	0.1695	0.1545
B. Date of first egg of pausing birds		.2782	−.0754	−.3582	.2491	.1853
C. Date of pause onset			.0940	−.3552	.1389	.0929
D. Frequency of pause				−.4336	.7492	.6796
E. Duration of pause					−.4840	−.1023
F. Percentage of birds pausing						.8786
G. Degree of pausing						

[1] r at $P=0.05$ is 0.482; r at $P=0.01$ is 0.606.

Some differences may be also noted between the two populations with respect to the magnitude of the correlation coefficients between the different pause characters of sire families in the two populations. Table 9 lists the coefficients for the K population corresponding to those for the J series in table 6. There is agreement between the two tables as far as the majority of the correlation coefficients is concerned. There are, however, a few notable differences. Thus, while frequency of pause shows no correlation with percentage of birds pausing (−0.1733) or with degree of pausing (−0.0265) in the J series, in the K population the respective coefficients are 0.7492 and 0.6796. This changed relation also brings about differences in the coefficients of correlation between duration of pause and percentage of birds pausing (−0.4840 for the K series as compared to 0.1476 for the J) and between duration of pause and degree of pausing (−0.1023 for the K series and 0.5869 for the J). The coefficient of multiple correlation between degree of pausing on the one hand and frequency of pause, duration of pause, and percentage of birds pausing on the other is somewhat higher in the K series (0.9560) than in the J (0.9225), the former yielding 91 percent determination. Percentage of birds pausing seems to be the factor of major importance in accounting for differences in the degree of pausing in both of the series. This suggests that in breeding against occurrence of winter pausing the percentage of pausing birds, rather than duration or frequency in a family might be used as the standard of selection.

The general picture obtained from analysis of the J series is not particularly changed by the addition of the data for the K population. The fact that some of the relations between pause characters of sire families are different in the two populations argues for the point of view that the relations vary with the degree of pause observed.

The results from repetitional matings in the 2 years for which the data are considered may be of some interest. Table 10 presents the pause characteristics of the progeny of males mated in both years, as well as the performance of full sisters hatched in the 2 years. Only those matings which produced five or more sisters in each of the series are listed. It is apparent from this table that while the degree of pausing is higher in the J series, there is no consistent difference in either frequency or duration of pause between the J and K pullets. The percentage of birds pausing is, however, invariably greater in the J series sires' progeny and in full-sister families. This confirms the interpretation placed on the correlation coefficients. The same is true for all but one of the full-sister families with respect to degree of pausing.

It may be noted that for all of the repetitional matings the incidence of pausing birds is reduced 35.7 percent in the K over the J series. For the whole flock the reduction is 34.1 percent. This suggests that the major factors responsible for a lower percentage of pausing birds in the K series are environmental in nature, rather than genetic.

In absence of controlled experimental results it is not possible to say what these factors may be. However, by comparison of the performance of birds from the repetitional matings presented in table 10 and from other available information, some of the possible reasons for the observed differences in pause behavior may be considered.

TABLE 10.—*Pause characteristics of repeat matings*

Sire or mating	Series	Total birds	Proportion of birds pausing	Pauses per pausing bird (frequency)	Average duration of pauses	Degree of pausing
		Number	*Percent*		*Days*	
G14	J	65	66.2	1.33	23.8	16.6
	K	35	37.1	1.38	28.6	6.9
G52	J	50	74.0	1.57	24.0	22.8
	K	29	44.8	1.38	28.4	10.8
H33	J	38	81.6	1.55	34.4	33.2
	K	32	43.8	1.57	35.7	14.1
H60	J	29	82.8	1.83	15.8	23.5
	K	42	78.6	1.67	18.2	18.8
H90	J	66	63.6	1.31	35.4	20.6
	K	59	39.0	1.43	23.2	9.0
G14♂F424	J	6	33.3	1.50	14.3	5.7
	K	6	16.7	1.00	25.0	3.6
G14♂G738	J	9	55.6	1.60	25.5	17.5
	K	5	20.0	2.00	9.0	1.5
G14♂G742	J	12	58.3	1.29	12.6	5.1
	K	7	42.9	1.00	44.8	7.3
G52♂H590	J	11	81.8	1.56	27.6	25.4
	K	6	66.7	1.75	9.3	8.1
H90♂G312	J	7	57.1	1.25	20.4	12.6
	K	6	33.3	1.50	20.7	6.8

As reported elsewhere (*9*), each of the two series was divided approximately evenly, so that one-half of the pullets of each mating were on one ration, and one-half on another. The difference between these rations was in the percentage of wheat bran in substitution for whole wheat, the percentage of protein and minerals being adjusted by other slight changes. One ration was common to both series. Despite differences in age at sexual maturity between the groups on different rations in the J series, there was no difference in the extent of winter pause. The K series on the whole exhibited earlier sexual maturity than the J series, though no difference was found in age at first egg of pullets on the two rations used in the K series. However, sexual maturity cannot be considered as a differential factor between the two series, since as shown in table 5 it has little bearing on the characters determining the degree of pausing. The difference in maturity between pausing and nonpausing birds within families existing above, if effective between series, would operate in the direction of increasing rather than decreasing the proportion of pausing birds in the K series above that of the J series.

There was no difference in extent or type of chick mortality in the repetitional matings of the two series, but the rate of growth was higher for the pullets of the K series. The average weight at 6 weeks of age in the repetitional matings was nearly 100 grams higher in the K series (342.1 grams against 248.1 grams in the J series). What bearing this observation may have on the nature of winter pausing cannot be determined from the data on hand.

So far as repetitional pausing of the same bird is concerned, there seems to be no consistent or significant difference between the duration of the first pause and that of the second (table 11). This was true for both the J and K series. There seems to be no evidence indicating that the second pause in birds pausing twice differs in any appreciable way from the first pause.

CLIMATOLOGICAL OBSERVATIONS

Seasonal curves for the total degree of pausing between November 1 and February 28 were drawn for each of the series and compared with the curves for precipitation, humidity, and maximum, minimum, and mean daily temperatures. These were drawn from data [4] recorded on the south bank of the canyon. The poultry plant is located on the north bank. No apparent relation between these climatological observations and the degree of pausing was apparent from these curves. Similarly, no apparent relation of the degree of pausing in the K series to daily hours of sunshine could be noted. The sunshine observations were made on the university campus about half a mile from the poultry plant.[5] No sunshine data for the year of hatch of the J series were available.

As far as the length of day is concerned, the degree of pausing in the J series varies inversely with the length of day up to the first period in December (December 1–10). In the mid-December period the degree of pausing begins to decrease while the length of day reaches its minimum. In general, the fluctuations in degree of pausing follow the changes in day length in a none-too-regular curvilinear fashion. This does not hold true for the K series, in which it appears that the degree of pausing fluctuates fortuitously as far as the length of day is concerned.

TABLE 11.—*Duration of pauses of birds pausing twice*

Series	Double-pausing birds	Duration of pause		First pause longer	Second pause longer	Two pauses of equal length
		First	Second			
	Number	*Days*	*Days*	*Number* [1]	*Number* [1]	*Number* [1]
J	136	23.1	20.2	73	58	5
K	55	22.3	24.5	27	26	2
Both	191	22.9	21.4	100	84	7

[1] Cases.

DISCUSSION

From evidence presented by Hays (*5*) and by the present writers, winter pause appears to be a character dependent upon both genetic and environmental conditions for its expression. The environmental agents producing a pause are seasonally determined but do not seem to be directly associated with any seasonal changes in the climatological factors studied. Evidence is available that pullet offspring from the same matings in different years respond differently with respect to pause. Since the genetic constitution of such groups of offspring would be expected to be very similar, the difference in incidence of pause might be presumed to be related to differences in environmental conditions between the years.

However, the intrinsic susceptibility of birds to pause does not seem to be constant. With increasing age at the season of the modal pausing period (effect of hatching date) and with increasing time in production preceding this period, there appears to be induced in the bird a physiological condition causing it to respond more readily to

[4] Supplied through the courtesy of C. J. Kraebel, of the California Forest Experiment Station.
[5] The sunshine observations were made available to the writers by Prof. John B. Leighly, of the Department of Geography of the University of California.

the environmental stimuli by pausing. Birds with different genetic constitutions show different responses to the same age, production, and environmental effects.

It is possible to conceive of winter pause as being induced by adverse environmental conditions which overcome the resistance of the bird to such external influences. The threshold of response varies with different birds at the same time and under the same conditions, and within the same bird at different times. Once induced, the pause proceeds for a period of time that does not seem to be related to the incidence of pausing in the flock or to the frequency of pausing in the bird. In the case of repetitional pausing, the course of the second pause does not seem to differ from that of the first pause. The duration of extremely long pauses might conceivably express the action of either repeated or continuous periods in which the effect of the adverse environment was above the threshold of response for the individual bird.

The distribution of pauses by 10-day periods between November and February indicated, in the case of the population with the high degree of pause, a uniform modal pausing period irrespective of the date of hatch. In the case of the population with a low degree of pausing, multimodal distribution prevailed, but the major modes in three out of four hatches fell in the same period as did the modes in the other population.

The seasonal distribution of pausing in the progenies of different sires showed considerably uniformity.

Date of pause onset and duration of pause depended largely on the date of first egg in the population as a whole, though no such relation is observed when sire families are considered.

Percentage of birds pausing depended to the greatest extent on date of hatch.

In birds pausing twice, there was no apparent difference between the duration of the first and of the second pauses.

The variation within the year in climatological factors studied did not seem to bear any direct relation to the degree of pausing in either population.

If the foregoing assumptions are true, the character of winter pause, observable only by its presence or absence, may in fact be genetically or physiologically governed by a wide range of variation in response thresholds. It is not likely that this concept of the basis of production of winter pauses can be proved by study of the production records of birds. Physiological studies identifying the changes in the birds associated with changes in thresholds of response would seem to be a more likely means of solution of the problem.

GENERAL CONCLUSIONS

Degree of winter pausing as defined here (percentage of hen-days from November to February spent in pauses of 7 days' duration or longer) is determined by the percentage of birds pausing in a population, by the frequency of pauses, and by duration of pause.

Percentage of birds pausing is of major influence in determining the degree of pausing in a population.

In a population with 21.9 as the degree of pausing, duration of pause was significantly correlated with degree of pausing, while in a popu-

lation with 11.4 as the degree of pause, frequency of pause was of greater importance than duration of pause.

Percentage of pausing birds in a family is suggested as a standard of selection in breeding against occurrence of winter pause.

Degree of pausing depends also on the genetic constitution of the birds (as shown by variance between sires), on the date of hatch, and on the season.

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THE ALLEGED PROTECTIVE ACTION OF ALFALFA AGAINST THE HEMORRHAGIC SWEETCLOVER DISEASE[1]

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INTRODUCTION

Reports of losses among cattle caused by the feeding of poorly cured sweetclover (*Melilotus*) hay appear annually. The disease induced by this fodder, often referred to as "sweetclover disease," is characterized by a diminished clotting power of the blood and, in the advanced stages, by severe hemorrhages which usually lead to the death of the animal. In a recent paper on one aspect of this problem Quick[3] concludes:

> Diet is the important means for controlling the disease. The incorporation of 5 percent of dehydrated alfalfa meal with the toxic hay was found sufficient to prevent the development of the disease or even any demonstrable reduction of prothrombin. * * * The animal [rabbit] appears to be able to store this accessory factor [from alfalfa], for it is very difficult to produce sweet clover disease in animals that have been fed relatively large amounts of alfalfa. This explains why some animals are far more resistant than others to the same lot of spoiled hay.

Quick points out the practical significance of these conclusions and calls attention to the possible relation of the above-mentioned accessory factor to the antihemorrhagic vitamin (K) required by the chick.[4] Quick's conclusions, however, are not in accord with the results obtained in the writer's studies of this disease.

VARIATION IN REACTION OF RABBITS TO TOXIC HAY

Schofield,[5] who earlier had called attention to the causal relation of spoiled sweetclover hay and silage to this disease, observed that young animals are more susceptible to the toxic principle than mature animals. This was apparent in the writer's early tests with rabbits. The studies of Roderick and Schalk[6] on this disease were made largely on cattle, but their tests on rabbits indicated that "a group of rabbits shows somewhat more variation in the time interval required for the disease to develop with a given hay than in a group of cattle." In the writer's experiments a marked variation in the response of rabbits of

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[2] The writer is indebted to Dr. R. A. Brink for suggestions and counsel in these studies.

[3] QUICK, ARMAND J. THE COAGULATION DEFECT IN SWEET CLOVER DISEASE AND IN THE HEMORRHAGIC CHICK DISEASE OF DIETARY ORIGIN. Amer. Jour. Physiol. 118: 260–271, illus. 1937. See pp. 263–264 and 269.

[4] DAM, HENRIK, and SCHÖNHEYDER, FRITZ. A DEFICIENCY DISEASE IN CHICKS RESEMBLING SCURVY. Biochem. Jour. 28: [1355]–1359, illus. 1934.

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similar age to a given toxic hay has been noted. Moreover, animals found susceptible in a preliminary test gave a similar reaction in subsequent exposures to the toxic principle, allowance being made for advancing age. The degree of toxicity of 15 samples of poisonous hay has been determined by pairs of rabbits found to be susceptible in a preliminary test, and in no instance has a significant difference been observed in the reaction of the two animals to any one hay. Furthermore, some rabbits have been included in as many as 10 trials with no apparent change in susceptibility other than that associated with advancing age. Some 150 rabbits have been used in these experiments.

Very few tests have been made on resistant animals, but one example may be cited. Six rabbits 6 weeks old were obtained from a local rabbitry in which no alfalfa was being fed. Toxic sweetclover hay was introduced gradually into the diet. For the first 2 days, the diet contained 15 percent of toxic hay, for the third day 40 percent, and for the fourth and fifth days 90 percent, the remainder of the diet in each instance being ground oats. Each rabbit received the oats and hay mixture in daily amounts of 45 gm. per kilogram of body weight. On the sixth day the clotting time of the blood of each rabbit was determined.[7] Of the six rabbits, three showed a blood-clotting time of over 60 minutes as compared with the normal 5 to 7 minutes; one, S6, showed a clotting time of 50 minutes; and two, S2 and S3, showed respectively 8 and 6 minutes. The four susceptible rabbits were transferred to nontoxic feed, while S2 and S3 were continued on the diet containing 90 percent of toxic hay for a further period of 7 days. During this period five tests of the clotting time of the blood were made, the highest value for S2 being 10 minutes and for S3 9.5 minutes, indicating a high resistance to the action of the toxic principle. After an interval of 86 days, during which S2 had been fed timothy hay and a mixed grain while S6 had been used in two tests for the toxicity of spoiled nonbitter sweetclover, the two rabbits were given an exclusive diet of toxic hay in daily amounts proportional to body weight. The data from this test shown in table 1 demonstrate that S2 maintained its resistance over an 86-day period on a diet devoid of alfalfa.

TABLE 1.—*Reaction of 2 rabbits, 1 resistant and 1 susceptible, when 6 weeks old, to an exclusive diet of toxic hay begun when rabbits were 20 weeks of age* [1]

Rabbit No.	Reaction when 6 weeks old	Blood coagulation of rabbit	
		Period on diet	Coagulation time
		Days	*Minutes*
S2	Resistant	0	6
		5	6
		10	5
		18	6
S6	Susceptible	0	5½
		[2] 5	25

[1] In the interval between the 6-week and 20-week tests, the diet of S2 was timothy hay and mixed grain; that of S6 after 5 days on toxic diet was timothy and mixed grain for 14 days, spoiled *Melilotus dentata* hay for 63 days, and timothy and mixed grain for 16 days.

[2] Ear hemorrhage from incision on fifth day; transferred to nontoxic diet.

[7] The determination was made as follows: Approximately one-half cubic centimeter of blood was allowed to drop from a freely bleeding incision in the marginal vein of the ear into a 50-mm. watch glass. Another watch glass was inverted over it, and the time required for the formation of a firm clot was determined at room temperature (23°–24° C.) by tilting the watch glasses at 30-second intervals.

The above data suggest that the variation in a group of rabbits in their reaction to a given toxic hay is due to the inherent characteristics of the animals and is not the result of previous feeding. No attempt has been made to test this interpretation further by the mating of resistant with resistant animals and susceptible with susceptible. In assembling a stock of rabbits for critical comparisons of the toxicity of various spoiled hays and extracts, the writer has adopted the procedure of subjecting a group of rabbits of similar age to a preliminary test on a known toxic hay. The animals showing a prompt response to the toxic principle are transferred to nontoxic feed in an early stage of the disease. The clotting time of the blood of these rabbits is normal when tested after an interval of 10 days and the animals are used in further experiments. In preliminary tests it became apparent that unless this variable of rabbit reaction is recognized and under control, an experiment involving a small number of unselected animals may be misleading.

ADDITION OF ALFALFA TO A TOXIC DIET

The writer has found no evidence in favor of the protective effect of small amounts of alfalfa. Roderick and Schalk [8] tested various vitamins and feeds, including alfalfa, on cattle with negative results. The writer has fed alfalfa up to 50 percent of the diet along with toxic hay and has observed the symptoms of the disease as determined by blood-coagulation tests. Moreover, a majority of the animals used in these experiments have received alfalfa ad libitum along with a grain mixture from the time of weaning until tested for reaction to toxic hay. No difficulty has been encountered in finding animals that react readily, and no significant differences in susceptibility have been found between groups of animals that received no alfalfa in the period prior to the preliminary test and groups that received alfalfa. Some experiments, however, have been made to test more fully the relation of alfalfa to the incidence of the disease.

In the first test a choice sample of commercial alfalfa hay, grading U. S. No. 1, Extra Leafy Extra Green was compared with a mixed grain for protective activity when fed as a supplement to a toxic sweetclover hay. Four rabbits that had been susceptible in early preliminary tests were first fed for 5 days on a known toxic hay in daily amounts proportional to body weight. The clotting power of the blood was then determined. After an interval of 9 days on timothy and mixed grain, two were put on a diet consisting of 10 percent of mixed grain and 90 percent of toxic hay and the other two on 10 percent of alfalfa and 90 percent of toxic hay. The results are summarized in table 2.

As will be noted in table 2, the clotting time of the blood from the rabbits when receiving supplement was determined after 5 days of feeding. Difficulty was encountered in arresting hemorrhage from the incision in the marginal ear vein in rabbits 2 and 4. To permit the disease to run a natural course, no further blood samples were taken and the ration was fed until the death of each animal. All four rabbits succumbed after a short feeding period and all showed hemorrhagic lesions typical of the disease. No significant difference in

[8] Roderick, L. M., and Schalk, A. F. See footnote 6

reaction was detected between the two pairs of rabbits and there was no suggestion of any protection resulting from the incorporation of 10 percent of a high-grade commercial alfalfa in the toxic diet.

TABLE 2.—*Effect of feeding susceptible rabbits toxic sweetclover hay, with and without supplement, as measured by the clotting power of their blood after 5 days of feeding*

Rabbit No.	Blood coagulation of rabbits fed—				
	Toxic hay		Toxic hay+supplement		
	Period on diet	Coagulation time	Supplement (10 percent of diet)	Period on diet	Coagulation time
	Days	*Minutes*		*Days*	*Minutes*
1	0	6½	Mixed grain	0	5½
	5	14		[1] 5	13
2	0	5½	Mixed grain	0	5½
	5	12		[2] 5	23
3	0	4½	Alfalfa	0	6
	5	17		[3] 5	15
4	0	4½	Alfalfa	0	5
	5	12		[1] 5	16

[1] Died of internal hemorrhages on 9th day.
[2] Died of internal hemorrhages on 13th day. Rabbit No. 2 consumed only small amounts of the ration from the 6th to the 10th day.
[3] Died of internal hemorrhages on 7th day.

One might, however, postulate that freshly cut alfalfa contains a protective factor which was inactivated during the curing or storage of the sample used in the foregoing experiment but preserved unimpaired in the alfalfa meal used in the experiment of Quick.[9] To obtain information on this point an experiment was made in which freshly cut alfalfa was used as a supplement to toxic sweetclover hay.

A 40-gm. lot of a poisonous sweetclover hay was fed to a susceptible rabbit. After an interval of 39 hours from the time of feeding, the prothrombin content of the blood was determined [10] by a modification of the method of Quick, Stanley-Brown, and Bancroft.[11] The prothrombin activity was found to have been reduced to 38 percent of normal. After a 21-day interval during which the prothrombin content returned to normal as determined by the above method, the animal again received 40 gm. of the same toxic forage and in addition 20 gm. of freshly cut alfalfa, which on a dry-weight basis constituted 12.9 percent of the ration. A test after 36 hours showed a prothrombin activity 42 percent of normal. In view of the regular response of susceptible animals to repeated treatments with the same toxic hay, it is apparent that the freshly cut alfalfa in the diet did not protect the animal against the action of the toxic principle.

Considerable interest has recently been shown in the artificial drying of legumes and grasses as a means of obtaining a product rich in accessory nutritional factors. A test similar to the one just described was made by using artificially dried alfalfa instead of the fresh forage.

Forty grams of toxic sweetclover hay along with 4.4 gm. (10 percent of the ration) of alfalfa dried for 3 minutes at 350° F. reduced the prothrombin activity in the blood of a susceptible rabbit to 45 per-

[9] QUICK, A. J. See footnote 3.
[10] The writer is indebted to H. A. Campbell, of the biochemistry research laboratory, for his cooperation in this and the following experiment.
[11] QUICK, A. J., STANLEY-BROWN, M., and BANCROFT, F. W. A STUDY OF THE COAGULATION DEFECT IN HEMOPHILIA AND IN JAUNDICE. Amer. Jour. Med. Sci. 190: 269–281. 1935.

cent; 40 gm. of the same hay with the same rabbit in the absence of a supplement gave a prothrombin reading of 48 percent. Obviously this alfalfa was ineffective in preventing the development of the disease.

SUMMARY AND CONCLUSIONS

Marked differences in the susceptibility of rabbits of similar age to the sweetclover disease have been observed in the course of experiments involving the assay of toxicity of various spoiled sweetclover hays. Animals shown to be susceptible in a preliminary test gave a similar reaction in subsequent tests although becoming progressively less susceptible with advancing age. Resistant animals, insofar as they have been tested, have maintained their resistance. It is suggested that this variation in a group of rabbits is an expression of the inherent constitution of the animals; there is no evidence in these experiments that the differences in the reaction of rabbits to a given toxic hay are induced by previous diet.

Experiments have been performed to investigate Quick's conclusion that alfalfa contains an accessory factor protecting animals against the sweetclover disease. A supplement of commercial alfalfa hay of excellent quality was fed to the amount of 10 percent of the ration along with a known toxic hay and compared with a supplement of mixed grain fed in like amount. Neither supplement gave any indication of retarding the progress of the disease.

Likewise freshly cut alfalfa to the amount of 12.9 percent of the ration of one susceptible rabbit and kiln-dried alfalfa as 10 percent of the diet of another showed no protective activity.

While Quick concludes that 5 percent of alfalfa in a diet of toxic sweetclover hay prevents the development of any symptoms of toxicity, the writer's results indicate that even 12 percent has no significant effect in checking the onset and fatal termination of the disease.

Because of these negative results in the control of the disease by alfalfa in rabbits, it would appear unsafe to attempt the control of sweetclover disease in livestock by the inclusion of a small quantity of alfalfa hay in a diet of sweetclover hay.

RELATIONSHIPS BETWEEN RAINFALL AND COFFEE YIELDS IN THE KONA DISTRICT, HAWAII [1]

By L. A. DEAN

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INTRODUCTION

The production of coffee in the Hawaiian Islands was begun more than a hundred years ago, although exports were not recorded until 1845. Since the turn of the century over 90 percent of the production has been centered in the Kona district on the island of Hawaii.

An inspection of crop census reports reveals large annual fluctuations in the amount of coffee produced in Hawaii. Controlled measurements made in conjunction with coffee fertilizer experiments have shown fluctuations in yield amounting to over 100 percent, suggesting some dominant climatic or growth factors. In the present paper it will be shown, by applying modern statistical methods of analysis to small samples of data, that coffee production in Hawaii is highly correlated with rainfall

THE KONA DISTRICT

The Kona district is a strip of terrain along the lee or southwest coast of the island of Hawaii, rising in a fairly uniform slope from sea level to 3,500 feet in approximately 5 miles. The coffee-producing area is a narrow belt about 22 miles long and 1 mile wide, ranging from 800 to 2,200 feet in elevation and consisting of small, fairly fertile pockets between relatively recent lava flows. At present, approximately 5,000 acres are devoted to the growing of coffee. The geological and geographical features of this area and its agriculture have been described by Powers, Ripperton, and Goto.[2]

The seasonal production of coffee in the Hawaiian Islands from 1900 to 1936 has been estimated by Cady, Maneki, and Murata.[3] The data from 1900 to 1920 were based on exports; those from 1921 to 1936 were based on the crop census reports of the Agricultural Extension Service, University of Hawaii. These data are recognized not to be precise estimates for the Kona district, as during the period not exceeding 5 percent of the total volume of coffee produced in the Hawaiian Islands was in districts other than Kona. Allowing for fluctuations in yield, there has been since 1900 a steady increase in the production of coffee in Kona, which may be attributed to the following factors: (1) Increased acreage, (2) increased age of the trees, and (3) improvements in fertilizer and cultural practices.

[1] Received for publication November 18, 1938. This investigation was supported in part by a special grant from the Territorial Legislature for coffee investigations in the Kona district.

[2] POWERS, H. A., RIPPERTON, J. C., and GOTO, Y. B. SURVEY OF THE PHYSICAL FEATURES THAT AFFECT THE AGRICULTURE OF KONA DISTRICT OF HAWAII. Hawaii Agr. Expt. Sta. Bull. 66, 29 pp., illus. 1932.

[3] CADY, H. B., MANEKI, M., and MURATA, K. COFFEE PRODUCTION IN HAWAII: A FIVE-YEAR SUMMARY OF COST AND EFFICIENCY STUDIES. Hawaii Univ., Agr. Ext. Serv. Cir. 32, 44 pp., illus. 1937. [Mimeographed.]

In the Kona district, coffee cherries mature and are harvested, for the most part, during the months from August through December. The blossoming season is in the early spring, usually from January through March. Each tree has two or more distinct periods of flowering, depending, supposedly, upon meteorological conditions.

FIGURE 1.—Primary lateral of a coffee tree in early spring showing simultaneous blossoming and spring growth.

During the spring, for 6 weeks to 2 months simultaneously with and following the flowering, occurs the maximum growth of laterals (wood which will blossom and bear fruit the following year). Thus the coffee tree is preparing for the next year's crop at the same time that it sets and develops the current year's fruit. This is illustrated

in figure 1, which shows a lateral with flowers and a flush of new growth.

RAINFALL DATA

Rainfall records at Kealakekua, which is fairly close to the center of the coffee area, are available for the years since 1891. Unfortunately, records for one station, at an elevation of 1,580 feet, were kept only until 1914, and those of a second station (elevation of 1,450 feet) which were available from 1901 proved not to be analogous during the overlapping 14-year period. For this reason only the second set of data is used in this study.[4]

The annual fluctuations in rainfall during the period 1901 to 1936 were leveled somewhat by obtaining running 5-year means, as

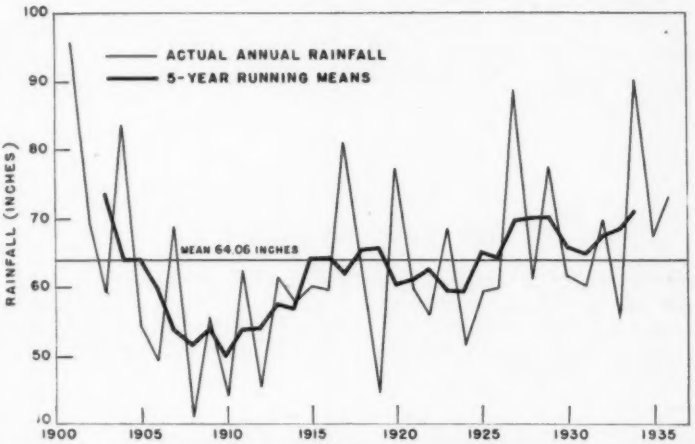

FIGURE 2.—Actual annual rainfall and 5-year running means of annual rainfall at Kealakekua, Kona, Hawaii.

charted in figure 2. It is evident that precipitation was distinctly heavy up to 1905 and from 1925 to 1936; from 1905 to 1915 rainfall was very light, and from 1920 to 1925 it was slightly subnormal.

The monthly distribution of rainfall expressed as means of a 36-year period and the standard errors of these means are given in the following tabulation:

Month:	*Mean rainfall (inches)*	Month:	*Mean rainfall (inches)*
January	3.68±2.83	July	[3] 6.88±2.30
February	3.28±3.98	August	[3] 6.99±2.15
March	4.02±2.40	September	[1] 7.48±3.25
April	4.92±3.16	October	6.06±3.22
May	[1] 6.48±2.82	November	[1] 3.71±1.74
June	[2] 6.67±2.69	December	3.88±3.73

[1] *P* value=0.05-0.02; [2] *P* value=0.02-0.01; [3] *P* value=<0.01.

These data show that the so-called rainy season in Kona is during the summer months; this is just contrary to what is common in most

[4] The rainfall records used in these investigations were obtained from the following: UNITED STATES WEATHER BUREAU. CLIMATOLOGICAL DATA. Hawaii Section.

districts of the Hawaiian Islands. It may also be noted that the months of high rainfall usually have significant means while those of low rainfall have not; in other words, the months having low mean rainfall have the most irregular rainfall.

EFFECT OF RAINFALL ON COFFEE YIELDS

The relationships between rainfall and yield of coffee (*Coffea arabica* L.) in Kona were studied by calculating partial regression coefficients and their sampling errors. The statistical methods used were those described by Fisher.[5] All regression equations included a term for time in years in order to eliminate the effects of an assumed linear increase in annual production resulting from increased acreage and age of trees and improved cultural practices.

At the outset it seemed desirable to determine whether rainfall directly affected current yield, or indirectly affected yield through the growth of laterals (fruiting wood). For this purpose the following three regression equations were used:

$$(y-\overline{y})=b_t(t-\overline{t})+b_{r_1}(r_1-\overline{r}_1) \quad (1)$$

$$(y-\overline{y})=b_t(t-\overline{t})+b_{r_2}(r_2-\overline{r}_2) \quad (2)$$

$$(y-\overline{y})=b_t(t-\overline{t})+b_{r_3}(r_3-\overline{r}_3) \quad (3)$$

where y=coffee production in million pounds per annum; t=time in years; r_1=annual rainfall occurring during the years of fruiting; r_2=annual rainfall occurring during the years of producing fruiting wood; and r_3=annual rainfall occurring during the years previous to the production of fruiting wood.

TABLE 1.—*Partial regression coefficients of coffee production on rainfall occurring during different years of the growth of coffee*

Equation No.	Annual (January to December) rainfall occurring during—	Partial regression coefficient
1	Years of fruiting (r_1)	0.0025±0.0176
2	Years of producing fruiting wood (r_2)	[1].0378± .0161
3	Years previous to years of producing fruiting wood (r_3)	.0062± .0153

[1] P value=0.05 to 0.02.

The partial regression coefficients calculated for the above equations and the standard errors of the coefficients are given in table 1. They show that the rainfall occurring during the year in which new fruiting wood is being produced is significantly related to the succeeding year's yield of coffee. In other words, the rainfall that is related to the seasonal fluctuations in coffee yield does not occur in the year of blossoming, maturing, and harvesting of the cherries. Having established that the rainfall occurring during the preceding crop year is related to the yield of coffee, the annual rainfall was divided into the

[5] FISHER, R. A. STATISTICAL METHODS FOR RESEARCH WORKERS. Ed. 5, rev. and enl., 319 pp., illus. Edinburgh and London. 1934.

following three periods: e, Early rainfall from February to June; m, middle rainfall from June to October; and l, late rainfall from October to February. The relationships between each of these three periods of rainfall and the following year's yield of coffee were studied, the following regression equations being used:

$$(y-\overline{y})=b_t(t-\overline{t})+b_e(e-\overline{e}) \quad (4)$$

$$(y-\overline{y})=b_t(t-\overline{t})+b_m(m-\overline{m}) \quad (5)$$

$$(y-\overline{y})=b_t(t-\overline{t})+b_l(l-\overline{t}) \quad (6)$$

$$(y-\overline{y})=b_t(t-\overline{t})+b_e(e-\overline{e})+b_m(m-\overline{m})+b_l(l-\overline{t}) \quad (7)$$

The partial regression coefficients and their standard errors calculated for the above equations are given in table 2. It may be seen that

TABLE 2.—*Partial regression coefficients of coffee production on three seasons of rainfall in Kona*

Equation No.	Partial regression coefficients b on—				Standard error of partial regression coefficients of production (y) on—			
	Time t	Early rainfall e	Middle rainfall m	Late rainfall l			m	l
4	[1] 0.285	[1] 0.080			0.0179	0.0228		
5	[1] .279		0.054		.0211		0.0306	
6	[1] .277			0.045	.0205			0.0348
7	[1] .281	[1] .075	.0064	.0471	.0187	.0239	.0272	.0314

[1] P value=<0.01.

FIGURE 3.—Comparison of the actual coffee production of Kona with that estimated from the equation $y=0.285t+0.08e-1.67$ (where y=estimated production, t=time, and e=February to May rainfall).

only the rainfall occurring between February and June of the preceding season is significantly related to the annual yield. Substituting the calculated values in equation (4), we have

$$y=0.285t+0.08e-1.67$$

This equation was used in obtaining the estimated production of coffee given in figure 3. From the statistical significance of the partial regression coefficient of yield on early rainfall and the general agreement between actual and estimated productions, a considerable amount of the seasonal fluctuation in Kona coffee production may be ascribed to varying early rainfall.

Annual yields of approximately half an acre of coffee trees measured in conjunction with a fertilizer experiment are available for 8 years. Figure 4 shows the annual fluctuations in yield as compared with

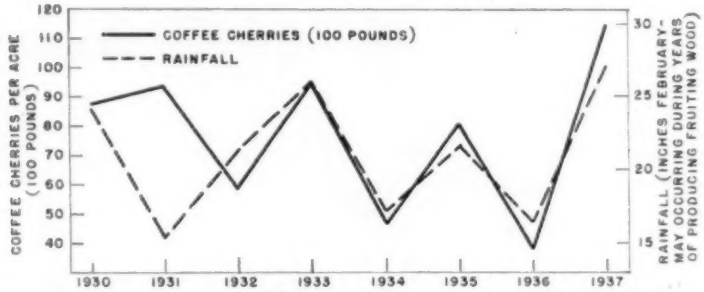

FIGURE 4.—Seasonal fluctuations in yields of a coffee fertilizer experiment, and February to May rainfall occurring during the years of growing fruiting wood.

annual fluctuations in early rainfall occurring during the years of growth of the fruiting wood. It may be seen that, with the exception of 1 year, the fluctuations are concordant. Because of the limited number of observations, statistical methods were not applied to these data.

SUMMARY

Statistical analyses of data on rainfall and coffee production for the years 1901 to 1936 in the Kona district of Hawaii show two distinct periods of heavy rainfall and one period of markedly light precipitation.

The dry season occurs during the winter months, and the months that have low mean rainfall have the most irregular rainfall.

Much of the variability in annual coffee production may be ascribed to fluctuations in the February to June rainfall occurring during the years in which the fruiting wood was produced.

AN ANALYSIS OF GROWTH AND YIELD RELATIONSHIPS OF COFFEETREES IN THE KONA DISTRICT, HAWAII[1]

By J. H. BEAUMONT[2]

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INTRODUCTION

The cultivation of coffee (*Coffea arabica* L.) in Hawaii, in view of present world coffee economics, must undergo radical constructive changes if the industry is to attain economic stability. Cultural practices are haphazard and are not based upon practical or scientific principles. Fertilization may range from none to 2,000 or more pounds per acre. In many cases the composition of the fertilizer is not known, and usually applications are not made with consideration of the number of trees per acre, of size and vigor of trees, of previous or present crop, or of rainfall and other weather factors. Pruning may vary from none through that accomplished by the cane knife or machete to the extremely severe, detailed pruning periodically practiced with "topped" coffee.

Nevertheless, average annual yields per acre in Kona are high as compared with those of other countries, and a definite possibility exists that improved practices, based on careful analyses of tree requirements, responses, and yields in relation to the soils and climate of the district, would not only improve the quality and yield but also effect certain economies. The studies here reported were undertaken to secure precise information on the growth responses and yield of the coffee plant in relation to its environment and to serve as a basis upon which to construct more logical and profitable fertilization, pruning, and cultural practices for the district.

REVIEW OF LITERATURE

Growth and fruiting relationships of a number of economic tree fruits, particularly those of temperate-zone regions, have been given careful and detailed study. Trunk-circumference increase, length of terminal growth, length and diameter of fruit spurs, and other measurements have been employed by numerous investigators (Waring (*13*),[3] Collison and Harlan (*3*), HofMann (*8*), Overholser, Overley, and Barnhill (*10*), and many others). In general, circumference increase and terminal elongation in one growing season have been found to be correlated with the yield in the following year. In fact, it may be said that soil management, fertilization, pruning, thinning, and other important and expensive orchard operations are employed with consideration of their effects upon the crop of the following season as well as their effects upon the volume and quality of the immediate crop. Such studies and applications have not, so far as

[1] Received for publication November 18, 1938.

[2] The author is indebted to Dr. Lyman A. Dean for aid in securing certain of the growth records and for many helpful suggestions relative to the statistical treatment of the data and the preparation of the manuscript. Credit is due Ah Sin Char for her conscientious work in calculating and checking the statistics.

[3] Italic numbers in parentheses refer to Literature Cited, p. 235.

the writer is aware, been extended to the coffeetree nor to many other tropical fruit crops of commercial importance in Hawaii.

The effects of various climatic factors such as rain, frost, wind, etc., on fruit setting and biennial bearing are also well recognized with temperate-zone fruits. Auchter and Schrader (*2*), Hedrick (*7*), and Potter (*11*) have shown that frosts may be the causal factor in bringing about a biennial bearing condition of apple trees. Dean (*4*) has shown that spring rainfall is a powerful agent in determining annual variations in coffee yields in the Kona district of Hawaii. De Haan (*6*), who, however, presents very little quantitative data, discusses the effects of rain on flowering and fruit setting. While *Coffea arabica* may bloom at three or more successive periods, the peak of any bloom lasts only 1 day; thus it is entirely possible that certain climatic factors may be operative in Kona, as elsewhere, that induce the extreme annual fluctuations in yield reported by Dean (*4*) and shown in data reported by McClelland (*9*).

The literature on pruning and culture of coffee is extensive, but quantitative data on yields, quality, and grade of fruit are lacking except for those of McClelland (*9*), and perhaps others that have not come to the writer's attention. Alvarado (*1*) describes pruning systems developed and used in many countries, but again quantitative data on annual yields, costs of pruning and of harvesting, and quality of crop are not stressed. While as yet untested, the more important practices developed elsewhere, applied with a knowledge of climatic effects, tree growth, and fruiting behavior in the Kona district, may be expected to do much to increase annual yields and thus reduce cost of production.

GENERAL DESCRIPTION OF GROWTH HABIT AND MANAGEMENT OF COFFEETREES

The coffee plant, which is a small tree or shrub, has a distinctly dimorphic branching habit, as illustrated in figure 1. The vertical or main stem, as it elongates, produces opposite leaves at each node and a primary lateral shoot in the axil of each leaf. This lateral in turn produces opposite leaves and assumes a horizontal position. If the vertical is bent out at an angle from the axis of the tree, the terminal bud resumes growth in a vertical direction. To bend out a vertical or to cut it back will stimulate the growth of new vertical shoots along the stem immediately below the points of origin of the lateral branch (fig. 1).

Elongational growth of the lateral branch occurs through extension of the apical growing point and also through the formation of branches (secondary laterals) from vegetative buds occurring in the axils of the leaves. A cluster of one to four flower buds is also produced in the axil of each leaf, and each inflorescence produces one to four or more flowers, most of which set fruit. Flowering occurs during the spring rains at two or more periods, on new lateral growth only, produced the preceding growing season. Young trees or 3- to 4-year-old individual verticals of an older tree produce the greater portion of their crop on primary lateral branches; as the tree or vertical becomes older, increasing proportions of the crop are borne on secondary and tertiary lateral branches. In old trees it is impractical to distinguish between primary, secondary, or tertiary lateral growth in the main body of the tree as all are more or less comparable in growth and yield, while the

new primary laterals produced as the vertical elongates make up only a small proportion of the total bearing area of the tree.

The dominant system of training, particularly at medium and lower elevations in the Kona district, is to cut back or to bend over the

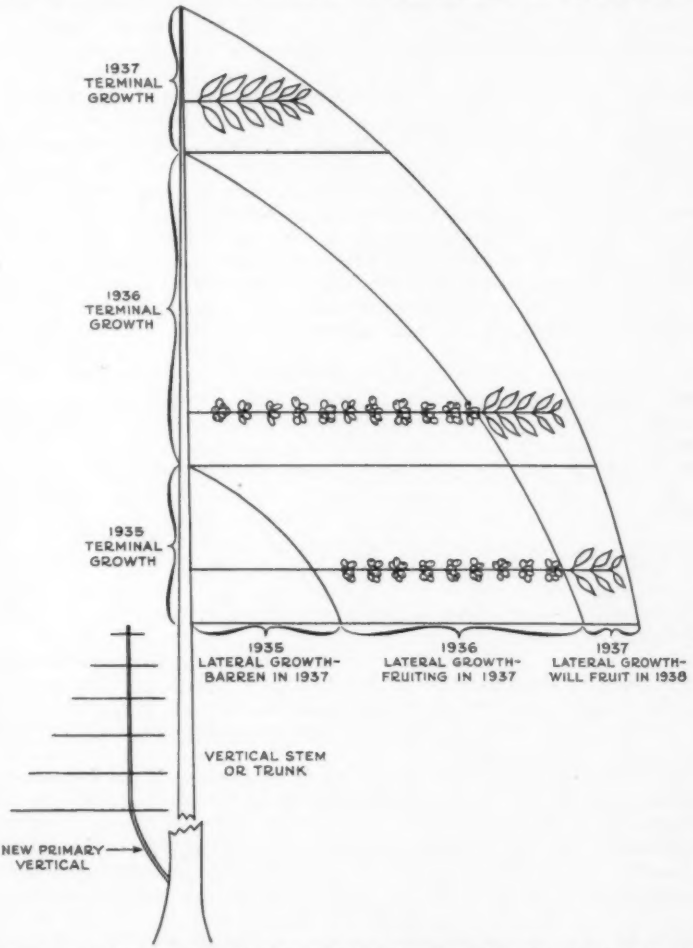

FIGURE 1.—Diagrammatic illustration of the growth and fruiting habit of the coffeetree. Normally two to four, or even more, verticals are trained to form the tree, in which case the primary and secondary lateral branches may overlap. The diagram is drawn to illustrate how biennial bearing may occur. Note the origin of a new vertical shoot. Normally this would not occur unless the old vertical were ringed, bent over, or cut off.

young (1- or 2-year-old) plant, thus stimulating the production of two, three, or even more verticals and training them into the bearing tree. Such a tree may be termed a multiple vertical and is the type used in

this study. Thereafter, little or no pruning is practiced, except removal of any superfluous new vertical shoots, until the tree attains an age and condition when it seems advisable to renew part of the tree by cutting out one of the verticals and training a new one to take its place. Thus, after the orchard has attained an age of 7 years or more, the trees become much less uniform so far as number and age of individual verticals per tree are concerned. No pruning, such as thinning out or heading back of the lateral growth of the tree, is normally practiced with multiple-vertical trees in the Kona district. Occasionally when trees become weakened through overcropping, lack of fertilizer, drought, or a combination of these, heavy heading back of the lateral branches similar to "parrot sticking" may be practiced.

A second general type of training is that of topping. This system consists of cutting off the vertical at a height of 5 to 7 feet above ground and consistently removing all vertical suckers so that the tree never attains a greater height. Growth and fruiting are confined to secondary and tertiary laterals. About once in 4 years the lateral growth is severely cut back with almost a complete loss of crop but with the development of strong new growth.

YIELD AND GROWTH DATA

The data to be used in an analysis of yield and growth relationships are obviously of the utmost importance. Unfortunately, the literature on coffee offered only suggestions as to the more responsive parts of the tree, measurements of which may be significantly correlated with yield, although growth studies of deciduous fruits were helpful. It was necessary to make numerous observations of the growth and cropping behavior of trees throughout the district and finally to take a number of measurements on a restricted group for the purpose of ascertaining their relative applicability and usefulness. Many measurements were discarded after inspection of the data and consideration of the ease and accuracy with which they could be duplicated. Others were not used because they were obviously highly correlated with other measurements (as, for example, the length of terminal growth and the length of primary lateral growth arising from the terminal growth) and consequently would not add materially to the total sum of information.

The coffeetrees used in this study were selected from two experiments: one established on the Fukuda farm, which was designed and installed by J. C. Ripperton, agronomist of the Hawaii Agricultural Experiment Station, to whom great credit is due for his foresight and early work with coffee (*12*); the other on the Akamatsu farm, which is supported in part by a special grant from the Territorial legislature for coffee investigations in the Kona district.

The preliminary measurements were made on the Fukuda trees; the Akamatsu trees were later selected for study. The following measurements, which are briefly described, were used in the analyses.

Yield: Individual-tree yields were secured and recorded in pounds and tenth-pounds; from four to six pickings over a period of 4 months were required. Only one annual yield (1937) was available for the Akamatsu trees; records for 2 years (1936 and 1937) were used for the Fukuda trees. Weights were obtained with a high-grade spring balance.

Average terminal growth: With the Akamatsu trees the 1936 average terminal growth was estimated by observing from the ground the

terminal growth of each vertical and using as a standard of comparison the 1-foot and ¼-foot divisions of a 12-foot pole employed in measuring tree height. With the Fukuda trees the 1936 and 1937 terminal growth of each fruiting vertical was measured with a flexible tape. Only verticals over 3 years of age were considered as fruiting verticals. The 2 years' terminal growth records were obtained in the same year (at the end of the 1937 growing season), as growth made in each year may be readily distinguished.

Lateral growth: On both the Akamatsu and Fukuda trees, the elongation of the fruiting laterals was obtained at the beginning of the 1938 growing season by measuring and averaging five or more apparently typical, readily accessible lateral growths borne in the larger fruiting area of the tree, at an elevation of 5 to 7 feet. Lateral growths arising from 2- and 3-year-old verticals that were not typical of the greater bearing area were avoided.

Total area of cross section of verticals: The sum of the squared circumferences of the several verticals of each tree was used in the statistical analyses as a means of expressing cross-sectional area. When area is specifically used in the text the appropriate correction factor ($1/4\pi$) was applied. The circumference of the vertical was obtained midway between the first and second nodes above the point of origin of the vertical. When the original vertical was intact it was measured at a point about 8 inches above the highest main vertical arising from it; in case no second vertical was present, the original vertical was measured at a smooth area on the trunk approximately 2 feet above the ground.

Statistical methods: The relationships between growth and yield of the coffeetrees at each of the two locations were estimated from the means and the simple and partial regression coefficients of the measurements. Sampling errors, calculated according to methods given by Fisher (*5*), were used to indicate the significance of the relationships studied.

THE EXPERIMENTAL TREES

Greater reliance may be placed on the relationship of any growth measurement to yield if it can be shown that the relationship persists with trees under different cultural, climatic, or other conditions. However, the labor and expense involved as well as the necessity of having the trees under control automatically restricted the study to two groups of trees. Under these conditions it seemed desirable to eliminate possible differences in soil, rainfall, elevation, etc., and to consider only the simpler contrasts of age and general vigor. The Fukuda trees had been under observation for some time and, consequently, the choice of a second group (the Akamatsu trees) was determined by the location of the first. The two plots are located near Kainaliu, North Kona. The soil is of approximately the same type, depth, and general physical and chemical characteristics at both locations. The distance between them is 1,000 to 1,500 yards and the difference in elevation only 75 to 100 feet, so that rainfall and temperature factors would be almost identical. The average elevation of the two is approximately 1,500 feet, the annual rainfall about 60 inches.

THE FUKUDA TREES

The Fukuda trees make up a fertilizer experiment, established in 1930, consisting of a 5 by 5 Latin square having nine trees per plot.

The trees were 12 years of age and had been under treatment 7 years when the present study was made. Fertilizer had been applied regularly at a basic rate of 160 pounds of N, P_2O_5, and K_2O per acre. A certain amount of renewal pruning, consisting of removing an old vertical and training a new one to take its place, had been practiced; consequently each tree contained one or more young verticals varying in age from 1 to 5 or more years. The trees had received little or no corrective pruning such as thinning out or heading back of the fruiting wood.

Potash proved to be a limiting factor in this experiment, as there are marked differences in growth and yield between those trees that received potash and those that did not (table 1). It may be seen that the potash-fertilized trees yielded approximately eight times as much fruit as the trees receiving no potash, the ratio being the same in both years in spite of the fact that the yield in 1937 was approximately three times greater than in the previous year.

TABLE 1.—*Size, age, and yield of coffeetrees grown under different fertilizer treatments—Fukuda experiment*

Treatment [1]	1936 yield per tree	1937 yield per tree	Average number of verticals per tree	Sum of total areas of cross section of verticals per tree	Average area of cross section per vertical	Sum of total ages of verticals per tree	Average age per vertical
	Pounds	*Pounds*	*Number*	*Square inches*	*Square inches*	*Years*	*Years*
NPK	17.0	58.0	2.8	9.33	3.3	18.5	6.6
NK	16.0	51.0	2.8	8.67	3.1	20.7	7.4
NP	2.7	8.5	2.5	4.36	1.7	14.4	5.8
N	2.7	5.0	2.5	3.83	1.5	13.2	5.3
No fertilizer (check)	3.7	8.8	2.4	4.07	1.7	13.7	5.7

[1] Fertilizers were applied at the rate of 160 pounds of each element per acre, one-half being applied in January and one-half in July of each year.

Visual differences in tree behavior between the potash and no-potash treatments are even more striking than may appear from the table. The no-potash plots invariably appear in poor foliage and the leaves are yellow and mottled even though the trees may be high in nitrogen. The lateral branches make very poor growth, and many die back to the vertical. Elongation as well as radial growth of the vertical after the first 2 years is slow, with the result that a 10- to 12-year-old vertical may be no longer and no greater in diameter than a 3-year-old vertical of a thrifty tree. Also, the verticals are weak structurally, as indicated by a tendency to bend over, even with very light crops.

In contrast, the potash-treated trees are extremely vigorous; their foliage is dark green and waxy, with little or no evidence of mottling, and persists, even on the 2-year-old lateral growth, until the fruit is ripe. Primary and secondary lateral growth is abundant and strong with little or no evidence of dieback. New verticals make strong heavy growth, especially when developing in full sunlight.

It may be seen from table 1 that there are no significant differences as yet apparent between the two treatments containing potash (NPK and NK). In later discussions of or reference to the Fukuda

trees, the potash-treated trees alone are considered. The no-potash trees were so poor as to be unsuited to the experiment planned.

THE AKAMATSU TREES

The Akamatsu coffeetrees were selected in 1937. They were carefully surveyed and the "off-type," replant, diseased, or other nontypical trees were discarded in order to reduce as much of the variability between the two groups as possible. Of these trees, 456 were amenable to relatively accurate measurement. The trees had been planted in 1930 and trained to a multiple-vertical system. Little or no renewal pruning had been practiced, and, in consequence, all the verticals were approximately of the same age. The trees had received no other pruning except that the lower lateral branches had been pruned off for a distance of about 4 feet above the ground. Practically no fertilizer had been applied during the 2 preceding years so that the trees were in relatively poor foliation and a low state of vigor and appeared to be deficient in nitrogen. Fertilizers were applied in July 1937, but since the rate was low and the trees were in full crop for the year it was thought that this fertilization would not affect the lateral and terminal growth of that season.

COMPARISON OF GROWTH AND YIELD MEASUREMENTS OF THE FUKUDA AND AKAMATSU TREES

The Fukuda and Akamatsu trees exhibit striking differences in growth and yield characteristics, as may be seen from table 2, in which the means of the growth and yield variates, with standard errors, are given. It will be noted that in 1937, which was a year of high yields, the Akamatsu trees yielded less than half as much as the highly fertilized Fukuda trees. The 1937 lateral growth was shorter on the Akamatsu trees in spite of the fact that they were younger and carried a much lighter crop. The 1936 terminal growth was considerably shorter which, although the yield for that year is unknown, is significant in view of the fact that the age of the trees was only 7 years as compared with the 12 years of the Fukuda trees. It will be indicated repeatedly, however, that the estimate of terminal growth of the Fukuda trees was influenced by the pruning practice.

TABLE 2.—*Means with standard errors of the variates used in the analyses of the growth and yield of the Akamatsu and Fukuda coffeetrees*

Variate	Akamatsu, mean	Fukuda, mean
1937 yield per tree.....pounds..	22.645±0.613	54.425±1.906
1936 yield per tree.....do....		17.015±1.144
1937 average lateral growth.....inches..	10.170± .111	12.322± .240
1937 average terminal growth.....do....		12.056± .498
1936 average terminal growth.....do....	13.050± .634	22.430±1.062
1937 total area of cross section of verticals per tree.....square inches..	9.803± .431	9.024± .496

The area of cross section of verticals, although the difference is not statistically significant, was somewhat greater for the Akamatsu trees than for those at Fukuda. This difference is doubless due to the fact that no renewal pruning had as yet been practiced on the Akamatsu trees and all or most of the fruiting verticals were 6 to 7 years of age, while the Fukuda trees had one or more young verticals on almost

every tree. The Fukuda trees, therefore, have a wider range in age of verticals, which is also expressed in the greater variability of the cross-sectional areas of the verticals per tree in proportion to the mean.

INTERRELATIONSHIPS OF GROWTH AND YIELD OF THE AKAMATSU TREES

The interrelationships of individual tree yield and growth responses of the Akamatsu trees were studied by calculating partial and simple regression coefficients and their sampling errors, the individual tree being used as a unit. The best simple expression of the independent relationships of yield on the several estimates of tree growth and size is provided by the partial regression coefficients (line 1, table 3) according to the equation

$$(y-\bar{y})=b_l(l-\bar{l})+b_t(t-\bar{t})+b_c(c-\bar{c})$$

where y=1937 individual-tree yield of cherry coffee in pounds;
l=1937 average lateral growth per tree in inches;
t=1936 average terminal growth of verticals per tree in inches;
and c=sum of the squared circumferences of verticals per tree in 1937 in square centimeters.

A number of the simple regression coefficients were calculated also and are given in table 3, lines 2 to 7, with sampling errors. A study of these coefficients, in relation to their sampling errors, shows that, with the exception of the regression coefficient of 1936 average terminal growth on the average sum of squared circumferences, all the coefficients are highly significant. The partial regression coefficients (line 1) indicate the independent relationships of the variates to the 1937 yield. For example, when the squared circumferences and 1936 terminal growth are held at their averages there is a negative relation between the yield (i. e., the developing crop) and the lateral growth produced in the same season. Likewise, when the squared circumferences and 1937 lateral growth are held at their means it is found that the 1937 yield is positively related to the previous season's (1936) terminal growth. Thus it is to be expected that the 1937 lateral growth would bear a negative relation to the 1936 terminal growth (line 5).

TABLE 3.—*Simple and partial regression coefficients of coffeetree measurements in various relationships, together with their standard errors—Akamatsu experiment*

Dependent variate	Regression coefficients (b) of dependent variate on indicated independent variates			Standard errors of regression coefficients		
	1937 average lateral growth	1936 average terminal growth	Average sum of squared circumferences per tree	1937 average lateral growth	1936 average terminal growth	Average sum of squared circumferences per tree
	Inches	*Inches*	*Square centimeters*	*Inches*	*Inches*	*Square centimeters*
1937 yield	[1]−1.933	[1]+0.605	[1]+0.027	0.205	0.111	0.002
			[1]+.028			.002
		+.801			.092	
1937 average lateral growth	[1]−2.312			.351		
			[1]−.0055			.0018
1936 average terminal growth		[1]−.292			.102	
			+.001			.001

[1] P value<0.01.

When other variates are held at their means, yield is positively related to size of tree as measured by the sum of the squared circumferences of verticals (line 1). However, it might be expected that annual increments of increase in area would be of more interest when these can be obtained. The simple regressions are of little interest considering the strong independent relationships indicated by the partial regression coefficients. It remains to be determined whether the 1937 lateral growth will bear a positive relationship to the 1938 yield.

INTERRELATIONSHIPS OF GROWTH AND YIELD OF THE FUKUDA TREES

The interrelationships of growth and yield of the Fukuda trees were studied also. The independent effects of the five growth and yield variates employed are provided by the partial regression coefficients in the equation

$$(y-\bar{y})=b_{y_1}\ (y_1-\bar{y_1})+b_l\ (l-\bar{l})+b_t\ (t-\bar{t})+b_{t_1}\ (t_1-\bar{t_1})+b_c\ (c-\bar{c})$$

where y=1937 individual-tree yield of cherry coffee in pounds;
y_1=1936 individual-tree yield of cherry coffee in pounds;
l=1937 average lateral growth per tree in inches;
t=1937 average terminal growth of verticals per tree in inches;
t_1=1936 average terminal growth of verticals per tree in inches;
and c=sum of square circumferences of all fruiting verticals per tree in 1937 in square centimeters.

These coefficients are given in line 1 and a number of the simple regression coefficients that were calculated are given in lines 2 to 15 of table 4.

TABLE 4.—*Simple and partial regression coefficients of coffeetree measurements in various relationships together with their standard errors—Fukuda experiment*

Dependent variate	Regression coefficients (b) of dependent variate on indicated independent variates					Standard errors of regression coefficients				
	1936 average yield per tree	1937 average lateral growth	1937 average terminal growth	1936 average terminal growth	Sum of squared circumferences per tree	1936 average yield per tree	1937 average lateral growth	1937 average terminal growth	1936 average terminal growth	Sum of squared circumferences per tree
	Pounds	*Inches*	*Inches*	*Inches*	*Square centimeters*	*Pounds*	*Inches*	*Inches*	*Inches*	*Square centimeters*
1937 yield	−0.158	[1] −2.822	[1] +1.378	+0.322	+0.782	0.174	0.759	0.473	0.203	0.367
	[1] −.627					.167				
		[1] −3.922					.742			
			[1] −1.500					.119		
				−.177					.192	
					+.481					.411
1936 yield				+.069					.116	
					−.001					.248
	[1] +.574					.132			.315	
1937 lateral growth				[1] +1.064						
					+.126					.335
	[1] +.168			[1] +.247		.043			.057	
1937 terminal growth										
					+.147					.107
1936 terminal growth					−.426					.226

[1] P value<.01.

Keeping in mind the age and vigor of these trees, an examination of the partial regression coefficients of 1937 yield (y) on each of the independent variates in turn when the other variates are held at their means, brings out a number of pertinent facts. The partial regression coefficient of the 2 years' yields shows that the 1937 yield is not proportionately related to the 1936 yield. Apparently the size of the 1936 crop sets up other tree reactions which may be either positively or negatively associated with the succeeding year's yield, and when these are held constant the yield per tree will vary more or less at random. This is borne out by the fact (line 2) that the 1937 yield, when considered in relation to the 1936 yield alone and without regard to other tree responses, is in significant negative relationship. From this relationship, the further assumption may be made that, no matter how great the yield of a tree, if other growth reactions can be maintained or increased, the yield in the succeeding year may also be maintained or increased, weather factors permitting.

Following this argument, the 1937 yield should be significantly and positively proportional to the 1936 terminal growth (lines 1 and 5) and the 1936 yield and 1936 terminal growth (line 6) should also be proportional. In contrast to significant coefficients obtained with the Akamatsu trees, these are not statistically significant. It is believed that with these older trees, particularly when verticals of widely different ages may be included in each tree, the vertical growth measurements made are not truly representative of the cropping capacity of the tree.

The strong negative regression coefficients of 1937 lateral and terminal growth on 1937 yield (lines 1, 3, and 4) indicate that in this year the generally heavy crop per tree had a marked influence on the length of growth in the same year and by inference on the potential crop of 1938.

When other variates are held at their means the 1937 yield per tree is related to size of tree as measured by sum of squared circumferences of fruiting verticals (line 1). However, with trees of this age and growth status it appears that seasonal variations in yield may not be estimated from size of tree as none of the simple regression coefficients (lines 6, 8, 11, 14, and 15) is statistically significant. This lack of correlation was mentioned in discussing the similar relationships with the Akamatsu trees, where, however, the simple regression coefficients were found to be statistically significant (lines 2 and 6, table 3).

DISCUSSION

The extreme differences in mean yields of cherry coffee of the Fukuda trees in the 2 years (1937, 54 pounds; 1936, 17 pounds) and between the Fukuda and Akamatsu trees in the same year are of considerable importance from the standpoint of a growth and yield study. While the data presented do not offer a full explanation or interpretation, as several important relationships were not obtained, the methods employed and the relationships found appear to have promise of value in interpretation of tree responses.

The 1936 terminal growth was the only growth measurement made that may be correlated directly with both 1936 and 1937 yields. Relationships of terminal growth and yield appear to have certain limitations, for with the Akamatsu trees, which are young and rela-

tively low in vigor, the 1936 terminal growth is significantly related to the 1937 yield, while with the Fukuda trees the 1936 terminal growth is related neither to the 1936 nor to the 1937 yields although the 1937 terminal growth is significantly related to the 1937 yield. It appears that the terminal growth of trees of the age and condition of the Fukuda trees is not a sensitive index of the actual yielding capacity except in a year of producing a heavy crop. During 1936, which was a light crop year and favorable for growth, the trees did not respond differentially in terminal growth as they did in 1937 with a much heavier crop. The terminal growth of a 12-year-old vertical which, under normal conditions is approaching maximum height, is relatively short even though the main body of the tree is making vigorous growth. Also, a number of these trees had been subjected to some renewal pruning (consisting of removing an old vertical, thus permitting a new vertical to grow and replace it), and by including in the average the growth of the younger verticals, the differences in growth of the older verticals and relationships with yield were obliterated. Thus terminal growth is an accurate index of the potential crop of the following year when younger, unpruned trees are used, but it does not apply to older trees which have undergone a certain amount of renewal pruning.

The strong negative regressions of 1937 lateral growth and 1937 yield of both the Akamatsu and Fukuda trees corroborate the negative terminal growth relationships found and are indicative of what may have occurred, in part at least, in 1936 to account for the difference in yield in the 2 years. All the fruit is borne on lateral wood, and in trees 12 years of age it is obvious, by inspection, that the greater bearing area is in the lower two-thirds to three-fourths of the typical tree. Therefore, the lateral growth in this area should, perhaps, be a better index of potential crop than the terminal growth even though the two are closely related, as may be seen.

Dean (*4*) has shown that the spring rainfall of the preceding growing season is a dominant factor in determining coffee yields in the Kona district. This can be explained by assuming that seasonal effects may be carried over from one season into the next through some growth and storage response of the plant. De Haan (*6*) indicates that flowering of the coffeetree is dependent upon spring rains. In the Kona district spring rains are most uncertain and irregular, as Dean (*4*) has pointed out. Thus, if light spring rains do not favor abundant flowering and fruit setting, the tree, carrying only a light crop, would respond to the fertilization and normal summer rains by producing abundant fruiting wood for the following season's crop. This phenomenon may have occurred in 1936 to account for the small yield of that year and the succeeding large crop in 1937. However, even with favorable conditions in 1938 it would seem logical to expect that the 1938 crop of the higher yielding trees of 1937 will be smaller because of the relatively poor growth made in 1937. This is supported by the strong negative regression of 1937 yield on 1936 yield per tree even though the 1936 yields on the average were far below those of 1937, and by the negative relationship of 1937 yield on 1937 lateral growth.

There is abundant evidence also that individual-tree condition and cropping ability are expressed, to a greater or less degree, in spite of favorable or unfavorable climatic factors which are usually general

in nature and affect an entire district. The striking regularity of "on" and "off" years, indicated by the data presented by Dean (*4*) and McClelland (*9*), suggests that an occasional extreme seasonal factor may set up a biennial-bearing tendency or rhythm similar to that of apples, reported by Auchter and Schrader (*2*), Potter (*11*), and others.

When all other independent variates are held at their means, the size of both young and old trees, as measured by squared circumferences of verticals, is clearly related to yield. The total area of cross section of verticals, however, does not appear to be as logical a basis for prediction of annual yields as, for instance, the annual increment of increase. Such a measurement may be expected to bear the same relationship to yield as lateral growth, or as terminal growth of young trees. This measurement may easily be obtained if proper precautions are taken. However, it cannot be used as readily in the field as the lateral or terminal growth. Annual increments of increase in area of cross section of other fruit trees have been found useful by many investigators.

The characteristics of the lateral growth have not been studied in detail, but observation indicates that the diameter and internode length of the lateral, the color and size of leaf at the node, and perhaps other factors may be related to the fruitfulness of the lateral. Thus the length is not necessarily the most important characteristic as, indeed, is obvious from the long willowy growths with long internodes and thin, light-green leaves that develop in the dense shade of the interior of the tree and seldom produce more than one or two berries at a node. A similar type of growth is found in closely planted orchards, particularly on the lower parts of the tree. These observations further emphasize the need of detailed examination of the tree and its response under different conditions in order that constructive and economically sound cultural practices may be developed.

CONCLUSIONS

This study of the yield and growth measurements of two groups of coffeetrees—the Akamatsu trees, which are 7 years of age and relatively low in vigor and production, and the Fukuda trees, which are 12 years of age and high in vigor and production—shows that, with minor exceptions, the same relationships exist in both groups. Thus it may be concluded:

(1) That certain growth responses of the tree are largely dependent upon or conditioned by the size or volume of the developing crop.

(2) That the volume of the crop is largely determined by the growth made in the preceding growing and crop season.

(3) That a dominant weather factor, such as spring rains, may disturb these relationships, as Dean (*4*) has shown, but the tree will resume its normal, overlapping, 2-year growth-and-bearing cycle in succeeding average years.

(4) That by judicious pruning and fertilization—the first of which would tend to reduce the current or immediate year's crop and both of which would tend to increase the production of vigorous fruiting wood—and perhaps by other cultural practices such as mulching which would tend to conserve moisture, the extreme fluctuations in annual yields may be reduced and the average yield as well as the general size and vigor of the tree may be considerably increased.

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